

LABROID INTRARELATIONSHIPS REVISITED: MORPHOLOGICAL COMPLEXITY, KEY INNOVATIONS, AND THE STUDY OF COMPARATIVE DIVERSITY

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ABSTRACT. The morphological and taxonomic implications of pharyngognathy in acanthomorph fishes are clarified, and the monophyly of the pharyngognath Labroidei is established. Characters bearing upon hypotheses of labroid intrarelationships are reviewed and a single minimum length tree is presented and discussed. Morphological character transformations within the Labroidei display a disconcertingly large amount of homoplasy and, until a single highly corroborated phylogeny is available, statements about relationships within the suborder must remain tentative.

The predominance of attributes of the pharynx and pharyngeal jaw apparatus as a major locus for character data in the diagnosis of the Labroidei is discussed, and the implications of pharyngeal dominance in systematic analyses are explored. Finally, we review the concept of the key innovation of labroid pharyngeal specialization as a causal explanation for the morphologic and taxonomic diversification of the Labroidei.

INTRODUCTION

The Labroidei, as conceived by Kaufman and Liem (1982), consists of the families Cichlidae, Embiotocidae, Labridae and Pomacentridae; together they include approximately 1,800 species (5–10% of all living fishes). The many ecological and evolutionary questions posed by the existence of species-rich, adaptively multiradiate, and often narrowly endemic communities of labroid fishes in tropical marine and freshwater biotopes occupy an important place in modern evolutionary studies (Futuyma, 1979; Greenwood, 1984; Stanley, 1979; Vrba, 1980; White, 1978).

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Systematists, ecologists, ethologists, geneticists, functional and evolutionary morphologists alike have probably focused on this group more than on any other neoteleostean clade. Within the last decade alone numerous publications have appeared dealing with questions of labroid development (Aerts, 1982; Claeys and Aerts, 1984; Morris and Gaudin, 1982), functional morphology (e.g., Dullemeijer, 1980; Dullemeijer and Barel, 1977; Gobalet, 1980; Liem, 1980, 1986; Liem and Sanderson, 1986; Strauss, 1984; Yamaoka, 1978, 1980), intrarelationships (e.g., Kaufman and Liem, 1982; Liem and Greenwood, 1981; Morris, 1982; Rosen, personal communication; Stiassny, 1980), ethology (e.g., Barlow and Munsey, 1976; Brett, 1979); and ecology (Hixon, 1980; Laur and Ebeling, 1983; Schmitt and Coyer, 1982; Witte, 1984).

Interest has also centered on the evolutionary dynamics of these fishes. To be open to scientific discussion and evaluation, however, hypotheses concerning the operation of evolutionary processes such as modes and rates of speciation, the acquisition and role of evolutionary novelties, and niche-space utilization need a corroborated and precise theory of phylogenetic interrelationships (Eldredge and Cracraft, 1980; Lauder, 1981, 1982a; Nelson and Platnick, 1981; Wiley, 1981). The concept of a coherent labroid assemblage has only recently emerged (e.g., Kaufman and Liem, 1982; Liem and Greenwood, 1981), and we are still far from a consen-

sus regarding the intrarelationships of this important clade.

Since the families comprising the Labroidei were originally united as the Acanthopterygii Pharyngognathy in the pre-darwinian classification of Müller (1843), attributes of the pharynx and pharyngeal jaw apparatus have played a singularly important role in labroid systematics. Our study further establishes the predominance of the pharyngeal jaw apparatus as the major locus for character data in the systematic diagnosis of the Labroidei and explores its possible implications in systematic analyses.

Recent research suggests that features of the pharynx, and in particular the labroid pharynx, have important evolutionary consequences not only for systematic studies, but for the diversification of the clade as well (e.g., Liem, 1973, 1980; Liem and Sanderson, 1986). It has long been speculated that intrinsic features of design can play a major role in evolution (Lauder, 1982b; Russell, 1982), and the key innovation of labroid pharyngeal specialization is a much cited explanatory case. We review the concept of the key innovation as a causal explanation for the morphological and taxonomic diversification of the Labroidei.

MATERIALS

Specimens were dissected under a Wild M-7 stereomicroscope, and drawings made with the aid of a camera lucida attachment. Osteological specimens were cleared and double stained following the procedure of Dingerkus and Uhler (1977). A complete list of materials including catalogue numbers is available from the senior author on request. Nomenclature of the muscles follows that of Winterbottom (1974) and Anker (1978). Topographical and skeletal nomenclature is based upon that of Nelson (1969), Rosen (1973) and Barel *et al.* (1976).

The following specimens were studied. Abbreviations in parentheses following species names refer to condition of speci-

mens examined: c.s. (=cleared and double stained) skel. (=skeleton) and alc. (=alcohol preserved).

Labroidei

Cichlidae: *Acaronia nassa* (c.s., alc.), "*Aequidens*" *coeruleopunctatus* (c.s., alc.), "*Ae.*" *potaroensis* (alc.), *Astatotilapia bloyeti* (c.s., alc.), *Astronotus ocellatus* (skel.), *Cichla ocellaris* (c.s., alc.), *Cichlasoma bimaculatum* (c.s., alc.), *C. (Heros) severum* (c.s.), *Crenicichla alta* (c.s., alc.), *Ctenochromis horii* (c.s., alc.), *Eetroplus suratensis* (c.s., alc.), *Geophagus surinamensis* (c.s., alc.), *Hemichromis bimaculatus* (c.s., alc.), *Oreochromis mossambicus* (c.s., alc.), *Orthochromis malagarensis* (c.s.), *Paratilapia polleni* (c.s., alc.), *Pelmatochromis buettikoferi* (c.s.), *Sarotherodon galilaeus* (c.s., alc.), *Tylochromis jentinki* (c.s., alc.)

Labridae: *Bodianus diplotaenia* (alc.), *B. rufus* (c.s.), *Coris julis* (alc.), *Crenilabrus melops* (c.s., alc.), *Halichoeres poeyi* (c.s.), *Labrichthys unilineatus* (c.s., alc.), *Labroides dimidiatus* (c.s., alc.), *Labrus bergylta* (c.s., alc.), *Lachnolaimus maximus* (skel.), *Pseudojulis notospilus* (c.s.), *Scarus* sp. (c.s.), *Sparisoma* spp. (c.s.), *Symphodus rostratus* (c.s.), *Tautoga onitis* (skel.), *Tautogolabrus adspersus* (c.s., alc.), *Thalassoma bifasciatum* (c.s.)

Embiotocidae: *Cymatogaster aggregata* (c.s., alc.), *Damalichthys vacca* (c.s., alc.), *Ditrema temmincki* (c.s., alc.), *Embiotoca lateralis* (c.s., alc.), *Hyperprossopon argenteum* (c.s.), *Hysterocarpus traski* (c.s.), *Micrometrus minimus* (c.s.), *Neoditrema ransonnetti* (c.s.), *Phanero-don furcatus* (c.s., alc.), *Zalembeius roseaceus* (c.s.)

Pomacentridae: *Abudefduf troschelli* (c.s., alc.), *A. saxatilis* (c.s., alc.), *Amphiprion allardi* (c.s., alc.), *Chromis atrilobata* (c.s., alc.), *C. cyaneus* (c.s., alc.), *Dascyllus albisella* (alc.), *Eupomacentrus planifer* (c.s.), *Microspathodon chrysurus* (alc.), *Neopomacentrus sindensis* (c.s., alc.), *Nexilaris taurus* (alc.), *Pomacentrus otophorus* (c.s., alc.), *P. moluccensis* (c.s.,

alc.), *Pristotis jerdoni* (c.s.), *Stegastes acapulcoensis* (c.s., alc.), *S. fuscus* (c.s., alc.)

Percomorph Outgroups

"Basal" Percoids

Centrarchidae: *Centrarchus macrop-terus* (c.s.), *Lepomis macrochirus* (c.s., alc.), *Micropterus dolomieu* (c.s., alc.), *M. salmoides* (alc.), *Pomoxis* sp. (c.s.)

Centropomidae: *Centropomus pecti-natus* (c.s., alc.), *Lates niloticus* (c.s.)

Lutjanidae: *Lutjanus blackfordi* (skel.), *Lutjanus synagris* (c.s., alc.), *Rhombolites aurorubens* (skel.)

Percidae: *Perca flavescens* (c.s., alc.), *Etheostoma olmstedii* (c.s., alc.)

Perchichthyidae: *Morone americana* (c.s.), *M. saxatilis* (c.s., alc.), *Perchichthys trucha* (c.s., alc.)

Serranidae: *Diplectrum radiale* (alc.), *Epinephelus striatus* (alc.), *Serranus cabrilla* (c.s., alc.), *S. fasciatus* (c.s., alc.), *S. hepatus* (c.s., alc.), *Synagrops bellus* (c.s., alc.)

Percoid Taxa "Close" to the Labroidei

Gerreidae: *Eucinostomus gula* (c.s., alc.), *Gerres cinereus* (alc.), *G. filamentosus* (c.s.), *G. poietii* (c.s.)

Haemulonidae: *Anisotremus virginicus* (skel.), *Anisotremus* sp. (c.s.), *Haemulon album* (alc.), *H. flavolineatum* (c.s., alc.), *Pomadasyd crocro* (c.s., alc.)

Kyphosidae: *Kyphosus* spp. (c.s., alc.)

Lethrinidae: *Lethrinus* spp. (c.s., alc.)

Sparidae: *Boops boops* (c.s., alc.), *Crenidens crenidens* (c.s.), *Diplodus vulgaris* (c.s., alc.), *Pagellus erythrinus* (c.s., alc.)

Scorpididae: *Scorpius chilensis* (alc.), *Scorpius* sp. (c.s., alc.)

Additional Percoid Outgroups

Apogonidae: *Apogon maculatus* (c.s.), *Cheilodipterus macrodon* (c.s.)

Bramidae: *Brama dussumieri* (c.s.)

Carangidae: *Caranx crysos* (c.s.), *De-capterus macarellus* (c.s., alc.) *Trachinotus* sp. (skel.)

Cepolidae: *Cepola rubescens* (c.s., alc.)

Chaetodontidae: *Chaetodon* spp. (skel.)

Pomacanthidae: *Pomacanthus paru* (skel.)

Cirrhitidae: *Cirrhitichthys maculatus* (skel.)

Girellidae: *Girella albostrata* (c.s., alc.)

Leiognathidae: *Leiognathus klunzingeri* (c.s., alc.), *Leiognathus* sp. (c.s.)

Mastacembelidae: *Mastacembelus brachyrhinus* (c.s.)

Mullidae: *Mulloidichthys martinicus* (c.s.), *Upneus maculatus* (c.s., alc.)

Mugilidae: *Agonostomus monticola* (c.s., alc.), *Mugil curema* (c.s., alc.)

Pempheridae: *Pempheris* sp. (c.s.)

Pomatomidae: *Pomatomus saltatrix* (c.s., alc.)

Sciaenidae: *Pogonias cromis* (c.s., alc.), *Menticirrhus americanus* (c.s.), *Otolithes ruber* (c.s., alc.), *Pseudosciaena axillaris* (c.s.)

Anabantoidei

Anabantidae: *Anabas testudineus* (c.s., alc.), *Ctenopoma multispinis* (c.s., alc.), *Sandelia capensis* (c.s.)

Belontiidae: *Betta pugnax* (c.s., alc.)

Blennioidei

Blenniidae: *Blennius gattorgine* (skel.)

Pholidae: *Aplodichthys flavidus* (skel.)

Gobioidei

Eleotrididae: *Gobiomorus dormitor* (c.s., alc.)

Gobiidae: *Bathygobius soporator* (skel., c.s.), *Gillichthys mirabilis* (skel.) *Gobius niger* (skel.)

Acanthuroidei

Acanthuridae: *Acanthus chirurgus* (skel.), *A. triostegus* (skel.)

Siganidae: *Siganus* sp. (c.s.)

Balistoidei

Balistidae: *Balistes* sp. (skel.), *Melichthys ringens* (skel.)

Tetraodontidae: *Tetraodon* sp. (skel.)

Diodontidae: *Diodon hystrix* (skel.)

Cyprinodontoidei

Cyprinodontidae: *Orestias cuvieri* (c.s.),
O. ispi (c.s.)

Fundulidae: *Fundulus diaphanus* (c.s.,
alc.)

Atherinidae: *Atherinops* sp. (c.s.),
Menidia menidia (c.s., alc.)

Exocoetoidei

Exocoetidae: *Exocoetus obtusirostris*
(alc.), *E. volitans* (alc.), *Cypselurus cy-
anopterus* (skel.), *Parexocoetus brachyp-
terus* (c.s., alc.)

Hemiramphidae: *Euleptorhamphus*
velox (alc.), *Hemiramphus balao* (alc.), *H.*
brasiliensis (skel.), *Hemiramphus* sp.
(skel.), *Hemiramphodon* sp. (alc.), *Oxy-
porhamphus micropterus similis* (alc.),
Hyporhamphus sajori (alc.)

Belonidae: *Ablennes hians* (alc.), *Bel-
one belone* (alc.), *Belone* sp. (skel.), *Pla-
tybelone argalus* (alc.), *Strongylura ti-
mucu* (alc.), *Tylosurus acus acus* (alc.), *T.*
crocodilus (alc.)

Scomberesocidae: *Scomberesox saurus*
(alc.), *Scomberesox* sp. (c.s., alc.), *Nanich-
thys simulans* (alc.)

METHODS

The size and intrafamilial diversity of labroid lineages, in combination with a lack of precise knowledge of intralinear relationships, makes selection of appropriate representatives problematical. For this reason, after an initial anatomical review within each major clade, we attempted to select a single taxon to represent the plesiomorphic familial condition for each of the characters or character complexes under investigation. Clearly it is not always the same taxon that bears the plesiomorphic state for each character under consideration (see also Stiassny, 1986). In addition to the data derived from the present review, a suite of characters relevant to the resolution of labroid

monophyly and intrarelationships was compiled from a comprehensive literature survey. For characters that have previously appeared in the literature we offer a reassessment of their value as indicators of phylogenetic relationship along with a citation of pertinent literature. Although all of the characters cited in previous analyses, as well as those novel to this study, are considered in the Character Survey section, we have been selective in those that we entered into the final analysis of labroid intrarelationships. Typically, a character was excluded from analysis for one of the following reasons:

1) We disagree with previous homology assessments; 2) The character distribution is highly variable and/or uninformative; 3) In one case, the distribution among outgroups is so variable as to render polarity determination highly problematical. Although several characters are excluded from our analysis, we include a discussion of these characters and make explicit our rationale for exclusion in each case. For ease of critical review we have included our data matrix in Appendix 1.

Throughout the study character polarity was assessed by the Outgroup Method (Maddison *et al.*, 1984; Stevens, 1980; Watrous and Wheeler, 1981). In the absence of a well worked-out scheme of labroid interrelationships, selection of appropriate outgroup taxa poses a problem. In view of the importance of outgroup designation in an analysis of this kind we have attempted to mitigate the situation by reviewing a wide range of percomorph taxa and selecting two groups of outgroup taxa for particular attention. The first group included representatives of some of the families thought to be "primitive" or "basal" perciforms (Gosline, 1966; Johnson, 1980, 1984; Regan, 1913; Stiassny, 1981). The second group included representatives of those families that have been suggested by previous authors to be "close" to the Labroidei. This group included members of the Sparidae and Gerreidae (Stiassny, 1980, 1981), Kyphosidae (Tarp,

1952), Scorpididae (Morris, 1982), Haemulonidae and Lethrinidae (Rosen, personal communication). In addition, we examined a further range of percomorph taxa including a number of other pharyngognathous acanthomorphs. Where possible, outgroup families are represented by the most morphologically generalized of their genera available to us.

A minimum length tree for the included data was derived using the branch and bound algorithm of PAUP version 2.4 (Phylogenetic Analysis Using Parsimony, Swofford, 1985) with Farris (1972) optimization. The tree was rooted by designating a hypothetical taxon representing an outgroup possessing the presumed primitive state for all characters included. All characters were coded as two state characters (see Appendix 1) of equal weight. In addition to computing the shortest tree, alternative topologies, of which 14 are possible, were also explored using PAUP (Swofford, 1985) and McClade version 1.0 (Maddison, 1986). For the purposes of our analysis we assumed familial monophyly for each of the component labroid families (Kaufman and Liem, 1982; Stiassny, 1980), and made no concerted effort to consistently sample the range of potential autapomorphies available for analysis. However, where a novel autapomorphy was identified we noted its presence and justified our assessment of its status. As the monophyly of the four major labroid lineages has been established previously (e.g., Kaufman and Liem, 1982), characters autapomorphic for the component taxa were not included in the intra-subordinal analysis.

LABROID MONOPHYLY AND THE CONCEPT OF PHARYNGOGNATHY

Despite a considerable amount of recent attention there remains much confusion about the morphological and taxonomic implications of what has been termed pharyngognathy in acanthomorph fishes (Kaufman and Liem, 1982; Liem and Greenwood, 1981; Morris, 1982; Ro-

sen, personal communication). A clarification of the concept, in particular as it has been applied to labroids, provides a helpful introduction to our investigation of labroid monophyly and intrarelationships.

The complex series of modifications of the pharyngeal jaw apparatus (PJA) resulting in the emergence of the mobile upper and lower pharyngeal jaws of euteleostean fishes has been well documented (Lauder, 1983; Nelson, 1967b, 1969; Rosen, 1973). Once that euteleostean level of organization was attained, the basic components were then available for subsequent modification along an impressive array of difference lines. Within the Acanthomorpha, perhaps in reflection of the high degree of pharyngeal modification exhibited by that clade, characteristics of the PJA have played an increasingly central role in attempts to elucidate phylogenetic interrelationships (e.g., Rosen, 1973, 1985; Rosen and Parenti, 1981).

Pharyngognathy, as originally conceived, is the possession of united fifth ceratobranchials. Gunther (1880), following Müller (1843), used pharyngeal morphology to characterize the order Acanthopterygii Pharyngognathii which he defined in part by the shared possession of "lower pharyngeal bones coalesced into a single unit." Numerous authors have questioned Gunther's interpretation of phyletic integrity, which included in the group pomacentrids, labrids, embiotocids, and cichlids (=chromides of Gunther, 1880), and many have proposed alternative classifications for these taxa (e.g., Berg, 1940; Bertin and Arambourg, 1958; Greenwood *et al.*, 1966; Jordan, 1905; Norman, 1966; Regan, 1913).

More recently, however, in a series of papers using a range of different approaches, Liem and his coworkers address the problems of pharyngognathy, labroid monophyly and interrelationships (Kaufman and Liem, 1982; Lauder and Liem, 1983; Liem, 1973, 1986; Liem and Greenwood, 1981; Liem and Osse, 1975; Liem and Sanderson, 1986). One result of this

work is the growing consensus that Müller's original grouping has phyletic integrity, a notion formalized by Kaufman and Liem (1982) with the assembly of these taxa into the Suborder Labroidei.

The Labroidei of Kaufman and Liem (1982) is defined on the basis of three pharyngeal characters: 1) Junction or fusion of the two fifth ceratobranchial bones into a single unit; 2) Diarthrosis (bone to bone contact) between upper pharyngeal jaws and the basicranium; 3) Presence of the sphincter oesophagi muscle as a continuous sheet, with no dorsal subdivision.

A review of these and other pharyngeal features enables us to refine the concept of labroid monophyly, and the use of the term pharyngognathy in morphological studies. Throughout this section summary statements of characters assessed to be synapomorphic for the Labroidei are italicized.

Among acanthomorphs there exists an array of diverse lineages each with representatives in which the pharyngeal jaws are hypertrophied (relative to non-pharyngognathous members of their respective clades), and the fifth ceratobranchials comprising the LPJ are united into a single functional unit. In addition to the labroids, Liem and Greenwood (1981) and Kaufman and Liem (1982) cited members of the Anabantidae (Figs. 1E, F), Kyphosidae, Pomadasyidae, Centrarchidae, Carangidae, Sciaenidae (Fig. 1A) and Cyprinodontoidei (see also Parenti, 1984) as bearing fused or otherwise joined lower pharyngeal jaws. Actually this list should be extended to include (some but not all) members of the Gerreidae (Fig. 1C), Leiognathidae (Fig. 1D), Sparidae and Haemulonidae (Rosen, ms), Pholidichthyidae (Springer and Freyhof, 1976), Lutjanidae (Johnson, 1980) and members of the Beloniformes² (Figs. 2B, C).

Comparison of the pharyngeal jaws in a range of percomorph taxa illustrates that the nature of the LPJ union differs markedly within the assemblage. In the majority of percoids with a hypertrophied pharynx the LPJ is formed by the close apposition of the two fifth ceratobranchials. The union is mediated by a simple straight suture reinforced ventrally by a concentration of connective tissue. This is also the case in the anabantoids examined (Figs. 1E, F). In pharyngognath gerreids (Fig. 1C) and sciaenids (Fig. 1A), as well as in virtually all cichlids (the single exception being the autapomorphic condition in *Cichla*, discussed by Stiassny, 1982 and in press), the suture is convoluted caudally and the contralateral elements interdigitate (e.g., Fig. 3B). Among cyprinodonts both the straight suture and the interdigitating type are expressed (see figures in Rosen, 1964; Rosen and Parenti, 1981). Finally, in the non-cichlid labroids (Figs. 3A, C, D), as well as in exocoetoid beloniforms (Figs. 2B, C), there is a complete fusion of the two LPJ elements and no trace of a central sutural union is evident. The phylogenetic implications of these different modes of union within the Acanthomorpha is unclear, although in the Labroidei the condition of complete fusion is interpreted as a synapomorphy of labrids, pomacentrids and embiotocids (page 288).

In view of the mosaic distribution of this character, the presence of coalesced lower pharyngeal jaws as a defining character of labroids is, by itself, rather weak (but see page 286 for further discussion). Indeed the "tendency" towards the expression of pharyngognathy (co-occurring with hypertrophy of the PJA) would appear to be extremely widespread

data are presented in Rosen (1964) and Rosen and Parenti (1981). The adrianichthyoids are notable among beloniforms in lacking a united and medially fused LPJ. Throughout this paper we adopted Rosen and Parenti's (1981) classification of the Beloniformes (Fig. 7; see also Collette *et al.*, 1984).

² Due to a lack of material available for examination, we have not included members of the family Adrianichthyidae in our analysis. Details of pharyngeal morphology of these fishes are few, but some

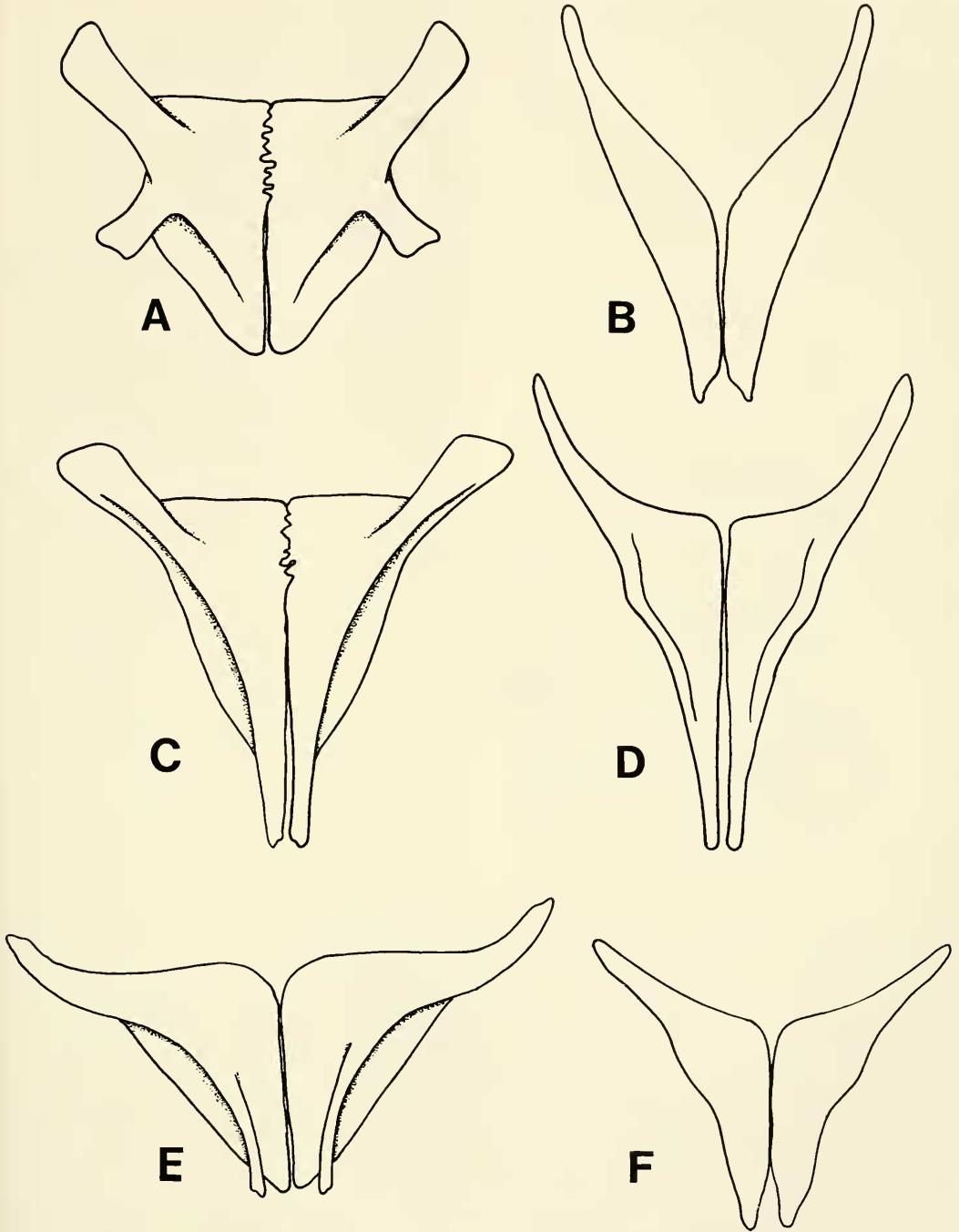


Figure 1. Lower pharyngeal jaw in ventral view. A. *Pogonias*; B. *Menticirrhus*; C. *Gerres*; D. *Leiognathus*; E. *Anabas*; F. *Sandelia*.

Abbreviations for this and the following figures are listed at the end of the text under Appendix 2.

among percomorphs, as well as in Rosen and Parenti's (1981) division II of the Atherinomorpha.

One feature of the LPJ appears to be unique (among perciforms) to the labroids and as such strengthens the claim of labroid monophyly. In all labroid taxa the LPJ bears a well-developed median keel on the ventral face of the bone (Fig. 3A-D). This blade-like keel serves as an attachment site for a part (or all, in some labrids and cichlids) of the transversus ventralis muscle (Fig. 4). Primitively among acanthomorphs the transversus ventralis is bipartite (TV V and IV), the second of these muscles (IV) passes from the fourth ceratobranchial of one side to insert on the contralateral element, thus entirely bypassing the fifth ceratobranchials (e.g., Fig. 4A). Although in a few other so-called higher percoid lineages the transversus ventralis is reduced to a single muscle (IV), in these taxa it passes between fourth ceratobranchials and has no insertion onto the LPJ keel. *The presence of a blade-like keel on the LPJ and the presumably correlated shift in insertion of part (or all) of the transversus ventralis onto that keel constitutes a synapomorphy of the Labroidei.*

In exocoetoid beloniforms a remarkably similar arrangement of pharyngeal keel and transversus ventralis insertion is present.

Primitively among perciforms the transversus dorsalis anterior muscle is bipartite and, following the nomenclature of Anker (1978), the two components are designated the m. cranio-pharyngobranchialis 2 and the m. transversus epibranchialis 2 (e.g., Figs. 5C, D). Within the Labroidei the percomorph muscle configuration has undergone a partial reduction and the *pomacentrids, embiotocids and labrids are characterized by the lack of the anterior muscle component, i.e., the m. cranio-pharyngobranchialis 2* (see Stiassny, 1980 figs. 22, 23, 24; Kaufman and Liem, 1982 fig. 2). A well-developed m. cranio-pharyngobranchialis 2 is pres-

ent in all cichlid taxa (e.g., Fig. 6E). An elaboration of the percomorph configuration of the transversus dorsalis is also evident among labroids and in cichlids (Fig. 6E), pomacentrids and labrids (Kaufman and Liem, 1982; Stiassny, 1980) a third division of the muscle is developed (the m. transversus pharyngobranchialis 2; Fig. 6E). Uniquely among acanthomorphs, the embiotocid transversus dorsalis anterior muscle complex is represented by a single component (the m. transversus epibranchialis 2). The embiotocid condition could have been derived by a reduction from the primitive bipartite percomorph condition or it could represent a reduction from the tripartite state of the remaining Labroidei. Although not strictly the most parsimonious interpretation, Stiassny (1980) adopted the second alternative. She regarded the presence of a m. transversus pharyngobranchialis 2 muscle division to be synapomorphic for labroids and interpreted the absence of the division in embiotocids as a secondary loss reflecting an extension of the reductive trend already noted in the loss of the cranio-pharyngobranchialis 2 of embiotocids, labrids and pomacentrids. Following the same reasoning, and with due reservation, we concur with Stiassny (1980) in her interpretation and assess *the presence of a m. transversus pharyngobranchialis 2 division of the transversus dorsalis anterior muscle to be a synapomorphy of the Labroidei (secondarily reduced in the Embiotocidae)*. However, the alternative interpretation of a cichlid/labrid/pomacentrid alignment based upon transversus elaboration is clearly posed.

According to Liem and Greenwood (1981) the Cichlidae are characterized by an additional subdivision of the m. transversus epibranchialis 2 (see Anker, 1978), resulting in a quadripartite transversus anterior muscle. The Labridae also bears a quadripartite transversus dorsalis anterior complex, but in these fishes the additional muscle part is a m. transversus epibranchialis (Stiassny, 1980). Reduction

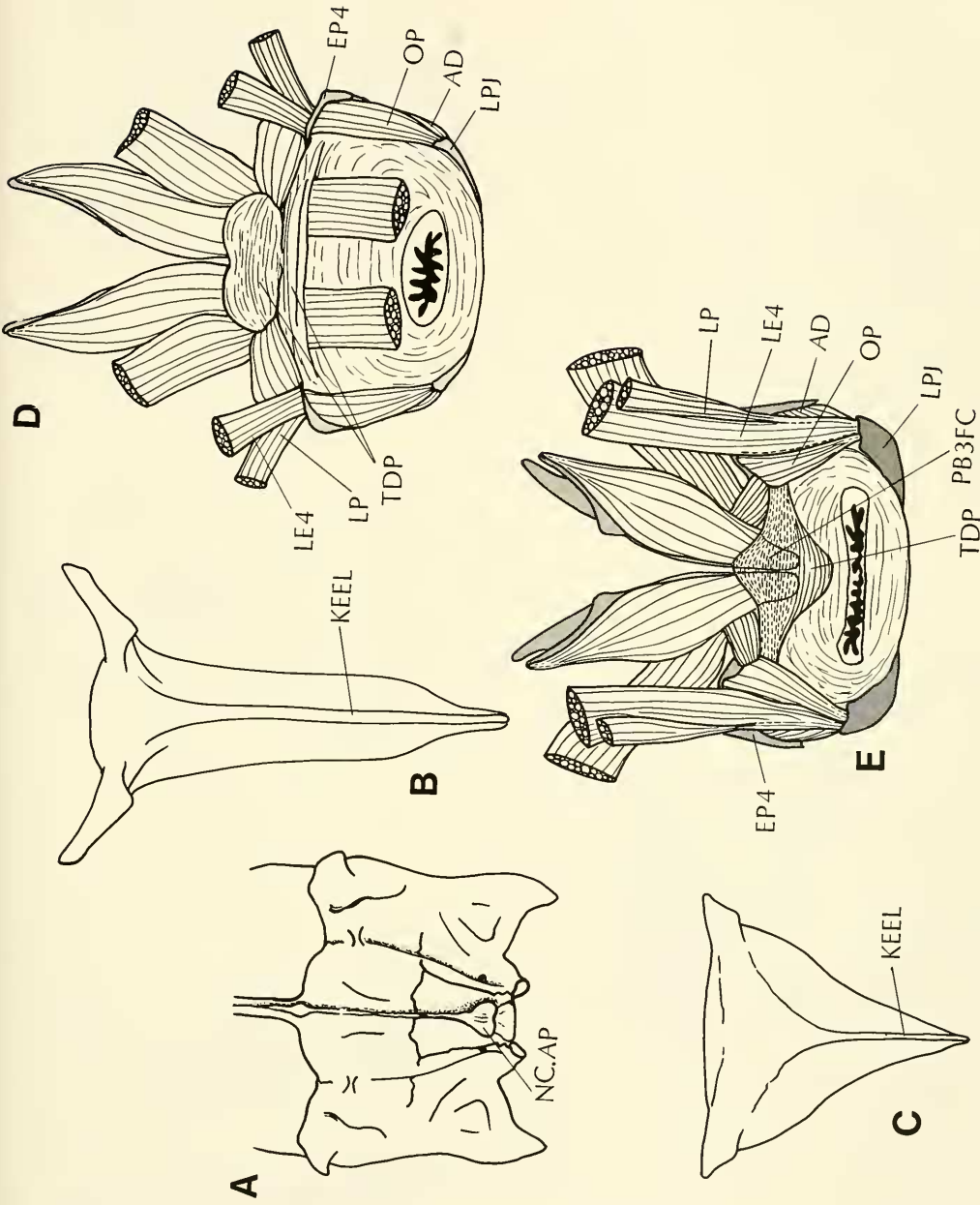


Figure 2. Aspects of the beloniform pharyngeal jaw apparatus. A. *Exocoetus* pharyngeal apophysis (ventral view); B. *Belone* LPJ (ventral view); C. *Exocoetus* LPJ (ventral view); D. *Strongylura* isolated PJA (dorsal view); E. *Exocoetus* isolated PJA (dorsal view).

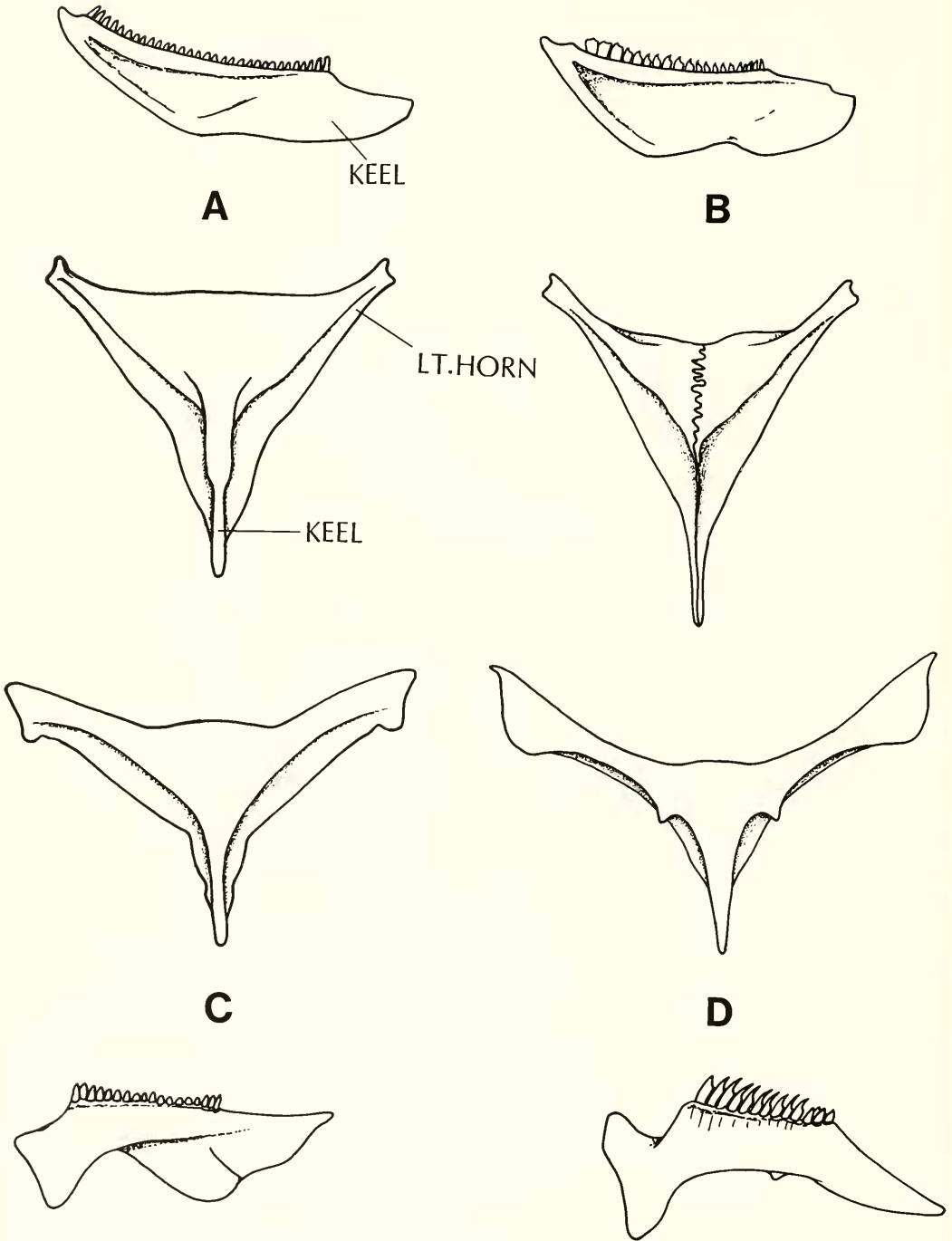


Figure 3. Lower pharyngeal jaw in lateral and ventral view. A. *Embiotoca*; B. *Astatotilapia*; C. *Labrus*; D. *Pomacentrus*.

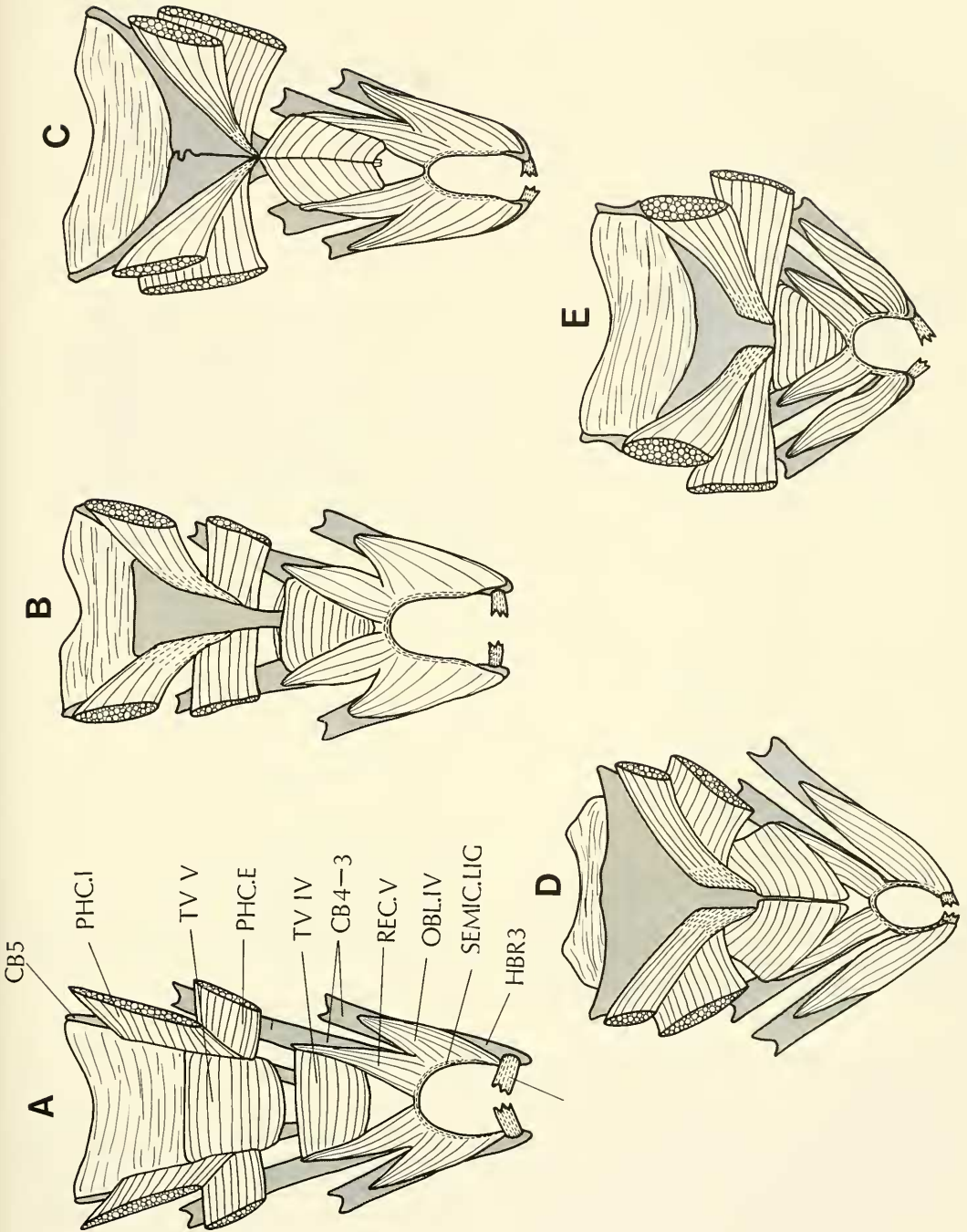


Figure 4. Ventral branchial arch musculature of: A. *Morone*; B. *Embiotoca*; C. *Astatotilapia*; D. *Labrus*; E. *Pomacentrus*, in ventral view.

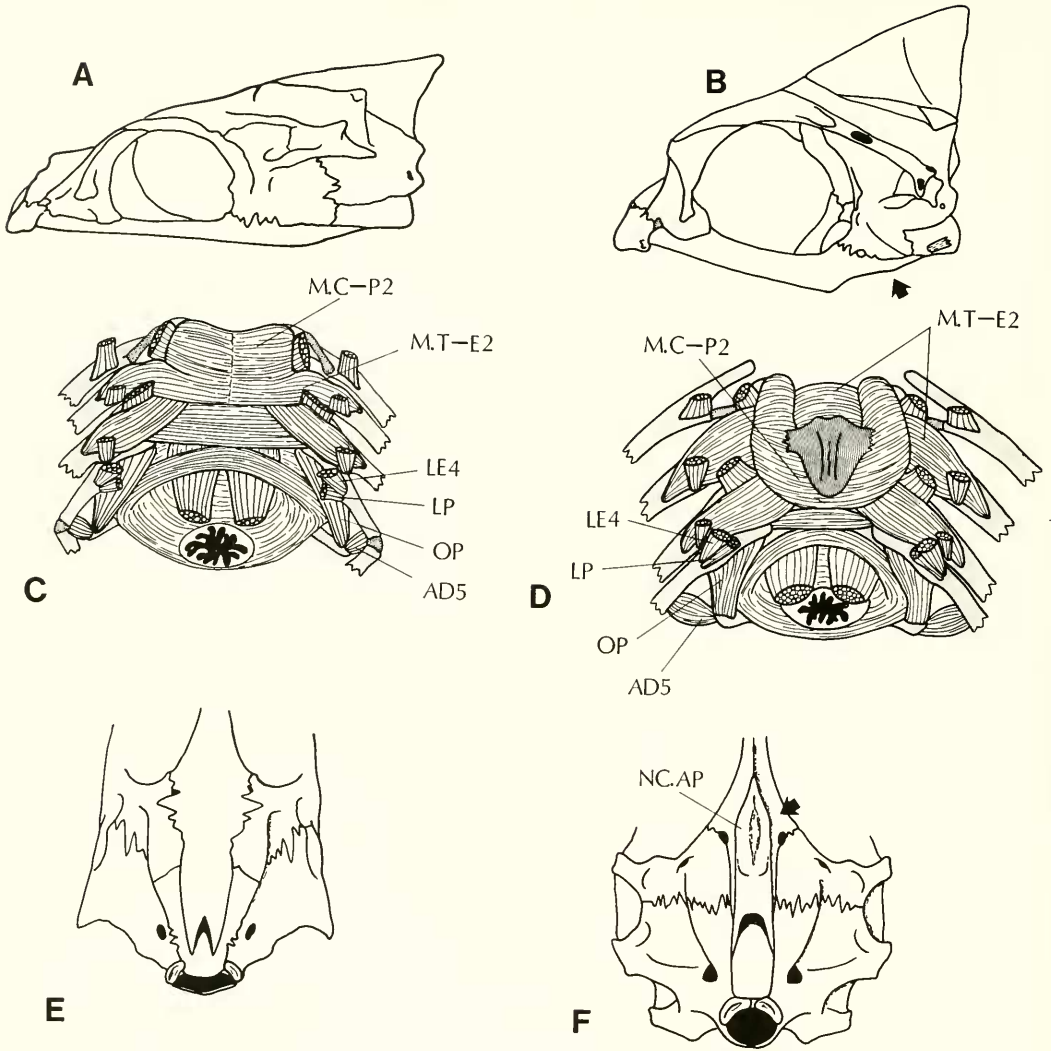


Figure 5. Aspects of the percoid pharyngeal jaw apparatus. A. *Morone* neurocranium (lateral view); B. *Diplodus* neurocranium (lateral view); C. *Morone* isolated PJA (dorsal view); D. *Diplodus* isolated PJA (dorsal view); E. *Morone* postorbital region of the neurocranium (ventral view); F. *Diplodus* pharyngeal apophysis (ventral view).

of the transversus dorsalis anterior to a single component—the m. transversus epibranchialis 2—is a synapomorphic feature of embiotocids.

Kaufman and Liem's (1982) second character, the presence in labroids of a true diarthrosis between upper pharyngeal jaws and the basicranium has been discussed by Stiassny (1980, 1982), how-

ever some additional clarification is helpful here.

In labroids the transversus dorsalis anterior and the transversus dorsalis posterior muscles do not completely overlie the raised articular facets borne on the third pharyngobranchials of the upper pharyngeal jaws (UPJ), and these bony facets are exposed (e.g., Fig. 6E; see also

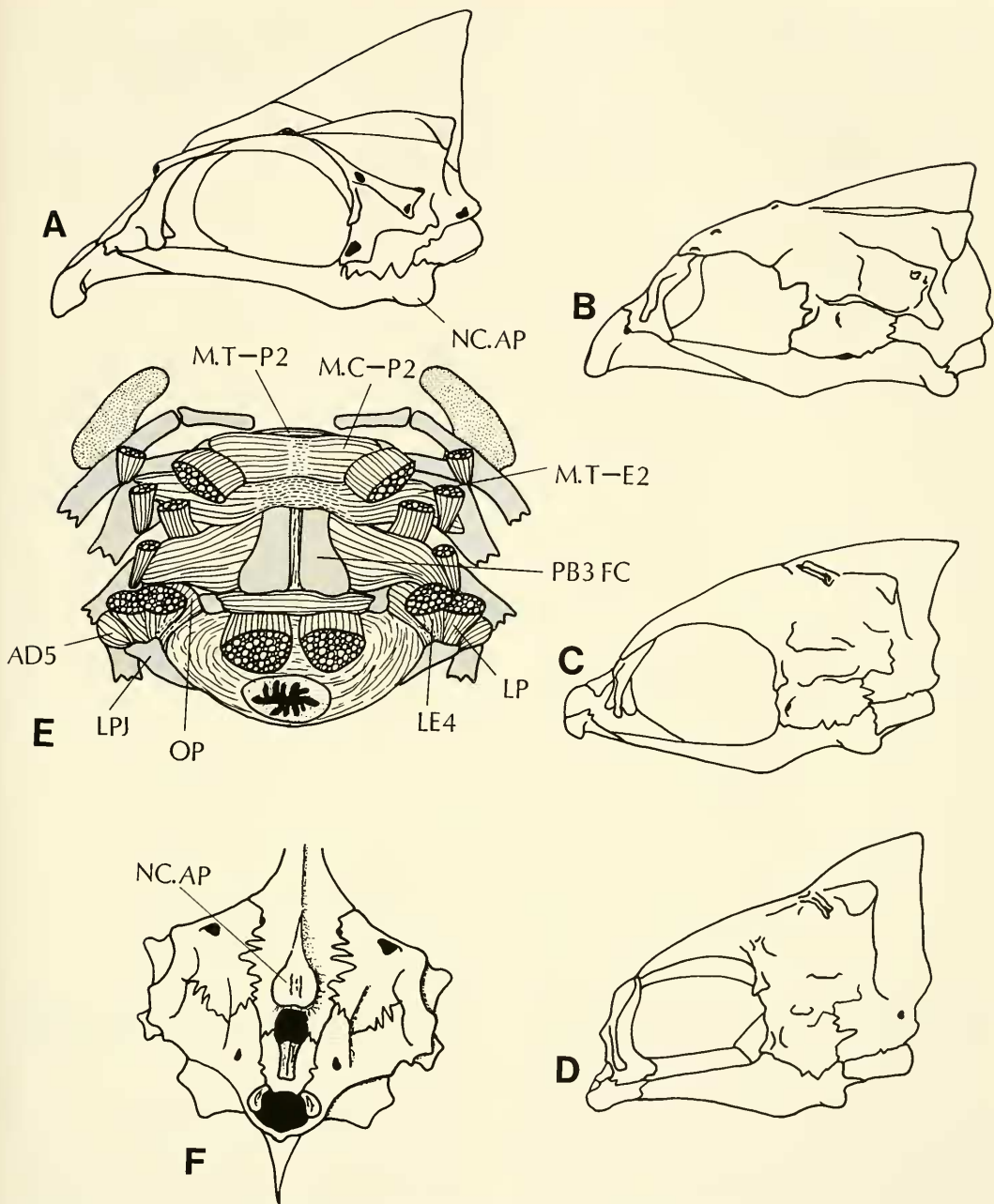


Figure 6. Aspects of the labroid pharyngeal jaw apparatus. A. *Tylochromis* neurocranium (lateral view); B. *Labrus* neurocranium (lateral view); C. *Embiotoca* neurocranium (lateral view); D. *Pomacentrus* neurocranium (lateral view); E. *Tylochromis* isolated PJA (dorsal view); F. *Tylochromis* pharyngeal apophysis (ventral view).

figures in Kaufman and Liem, 1982; Liem and Greenwood, 1981). On the skull base the LPJ facets are opposed by a raised neurocranial apophysis (Figs. 6A–D; see also Greenwood, 1978). This is not the case in “lower percoids” (e.g., *Serranus* Stiassny, 1982; *Morone*, Fig. 5C) where the entire dorsal face of the UPJ is covered by muscle and the skull base bears no articulatory or apophyseal structure (Fig. 5E). In pharyngognath members of the Gerreidae, Leiognathidae, Sciaenidae, Sparidae (e.g., Figs. 5B, D, F), and Girellidae a quite different situation pertains. In these taxa the transversus dorsalis anterior muscle complex is hypertrophied, and the cranio-pharyngobranchialis 2 forms a muscular “cushion” over the UPJ; the median connective tissue raphe, which is merely a longitudinal septum in *Morone* (Fig. 5C), is hypertrophied forming a substantial fibrous pad that overlies the muscle and is sculptured to fit closely into a grooved apophysis borne on the skull base (Figs. 5D, F). Although there is considerable variation in the form of the corresponding neurocranial apophyses, ranging from the strongly indented cup-like parasphenoid structure of *Pogonias* to the ventral thickening and reinforcement of the parasphenoid in *Diplodus* (Fig. 5F), in none of these taxa does the apophysis have the same morphology as that of labroids.

Based on these observations we consider the form of the labroid neurocranial apophysis highly characteristic of that clade. In labroids the articular surface is borne on a ventrally projecting apophysis formed in most cases by the parasphenoid and supported dorsally by the ventral margin of the prootic of each side. In some cichlids and embiotocids the basioccipitals also contribute to the articular surface of the apophysis (see Greenwood, 1978; Morris, 1982). In lateral view the apophysis of labroid fishes can clearly be seen as a rounded ventral projection (NC.AP in Figs. 6A–D). Greenwood (1978: 301) noted that the apophysis of certain labrids is structurally very similar to that of certain

cichlids, but concluded that “. . . the gross morphology is quite unlike that in the cichlids.” While we agree that the labrid apophysis is highly characteristic of that clade (see e.g., figs. in Rognes, 1973) we disagree that it is “quite unlike” that of other labroids. Thus, although a neurocranial apophysis of some form is commonly developed in other pharyngognath acanthomorphs, in no case is the apophysis developed in the same way or to the same extent as that described and illustrated here for the labroids. We propose that, in addition to sharing the synapomorphy of the presence of a true diarthrosis (bone to bone contact) between the neurocranial base and the third pharyngobranchials, *the labroids are further characterized by the synapomorphic presence of a ventrally projecting rounded form of the neurocranial apophysis.*

An interesting parallel is also found among beloniform fishes. In exocoetids (Exocoetidae and Hemiramphidae) a well-developed neurocranial apophysis (but formed entirely by the basioccipital bone) articulates with exposed dorsal facets on the third pharyngobranchials (Fig. 2A). The exposure of the third pharyngobranchials is brought about by a modification of the anterior portion of the transversus dorsalis posterior muscle into a thin connective tissue sheet (Fig. 2E). Contrasted with this is the condition of the complex in scomberesocids (Belonidae and Scomberesocidae) where, although a well-developed basioccipital apophysis is present on the neurocranium, articulation with the pharyngobranchial facets is interrupted by a thickened region of connective tissue of the transversus dorsalis muscle, as well as by the muscle itself (Fig. 2D).

The sphincter oesophagi muscle is subdivided in all of the nonlabroid percormorph taxa examined during the course of this investigation, and the lack of the subdivision is confirmed as being a synapomorphy of the Labroidei (Stiassny, 1980). The dorsal division of the sphincter oesophagi is greatly reduced (scombere-

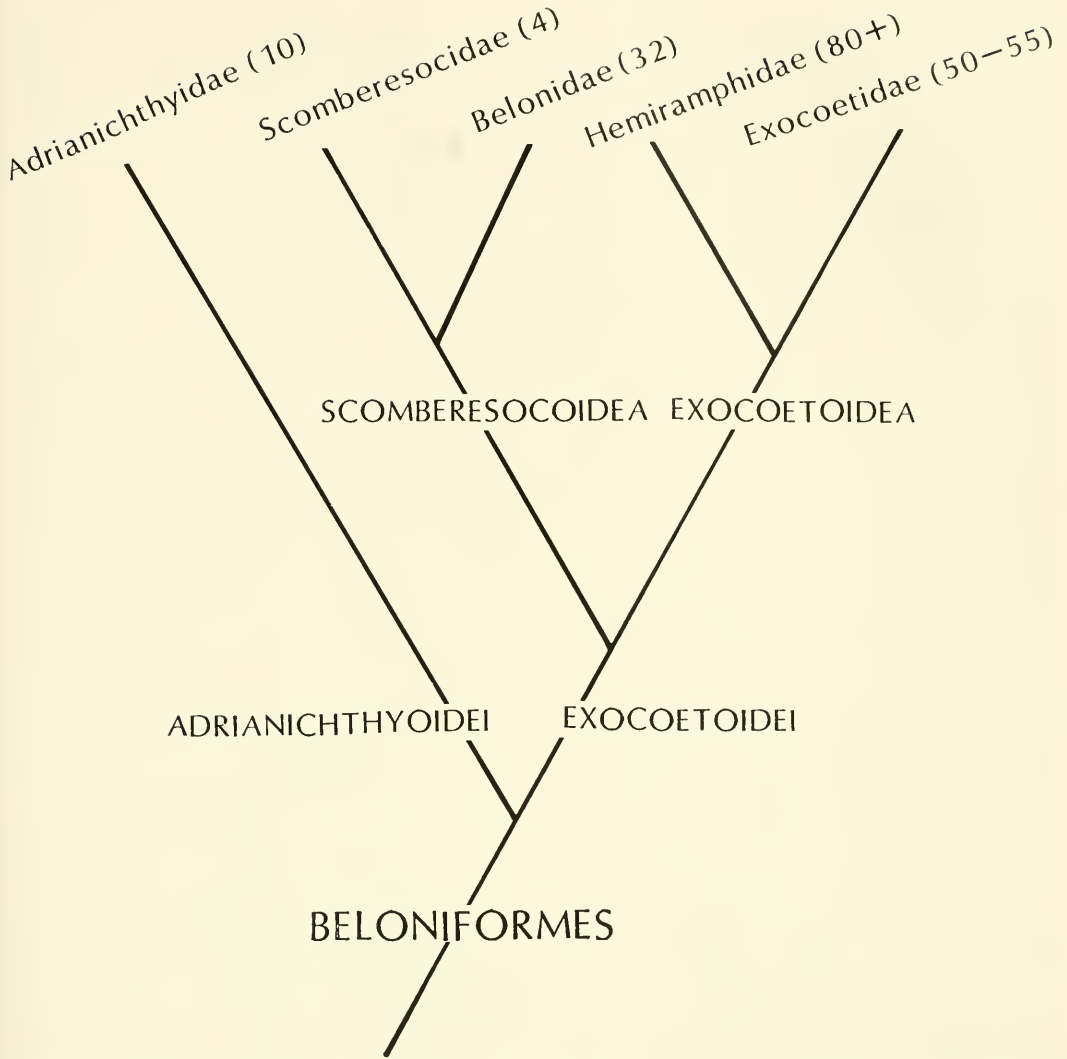


Figure 7. Cladogram of beloniform relationships, modified after Collette *et al.*, 1984. The numbers in parentheses after family names indicate number of included species.

socid), or entirely absent (exocoetid) in beloniforms. Before summarizing the principal components of this specialized labroid pharynx it is necessary to consider one further feature of the PJA.

Liem (1973) first drew attention to a fundamental difference in the muscular linkage between LPJ and neurocranium in cichlids as compared to other taxa (see also Liem, 1986). As part of the morpho-

logical basis for the adaptive radiation within the Cichlidae, Liem (1973) identified a functionally strategic shift in the insertion of the fourth levator externus muscle (le4) from the fourth epibranchial bone to the LPJ. A similar shift in levator insertion has since been found in labrids (including scarids and odacids) and embiotocids (Liem and Greenwood, 1981; Liem and Osse, 1975; Stiassny, 1980), and

the presence of this muscle sling has been thought to be central to the functional innovation of these taxa as well as being synapomorphic for the three families (Kaufman and Liem, 1982; Liem and Greenwood, 1981). The pomacentrids were thought either to entirely lack the le4/LPJ linkage (Liem and Greenwood, 1981) or possess a muscular sling in "its most primitive and incomplete configuration" (Liem, 1986: 311; see also Kaufman and Liem, 1982).

Our observations of the muscle sling in the Pomacentridae reveal a considerable amount of variation within that clade. In some taxa (e.g., *Neopomacentrus*, *Chromis* and *Amphiprion*; Fig. 8C) the configuration is much like that of other non-labroid percomorphs (e.g., Fig. 8A). While in others (e.g., *Stegastes*, *Dascyllus*, *Pomacentrus* and *Abudefduf*; Fig. 8B) the fibres of le4 are continuous, although interrupted by a fine myosept (see also Liem, 1986; Fig. 4 for the presence of a similar myosept in *Embiotoca*), with those of a division of the obliquus posterior. In those taxa in which the muscle sling is particularly well-developed (e.g., *Abudefduf* and *Stegastes*) the compound le4/obliquus posterior can be easily dissected free of the fourth epibranchial revealing a continuous connection between the neurocranium and LPJ, i.e., a true muscle sling.

From gross anatomical dissection it is not possible to determine exactly which components of the obliquus posterior muscle are incorporated into the compound muscle sling, and we have not undertaken an analysis of the ontogenetic transformations resulting in the compound muscle of pomacentrids. In view of this, the question of the homology of the resultant system with that of cichlids (Aerts, 1982; Claeys and Aerts, 1984), labrids and embiotocids (Liem, 1986; Liem and Sanderson, 1986) must remain open. The fact that a muscle sling is present only in some pomacentrid species poses problems for the analysis of this character at the level of the Labroidei.

Two possible interpretations suggest themselves based on this character distribution: 1) the pomacentrid muscle sling has been derived independently from that of the remaining labroids, or 2) a muscle sling is primitive for the Labroidei as a whole and has subsequently been lost within the Pomacentridae. Further information regarding the intrarelationships of the Pomacentridae may help resolve this question. For example, if the presence of a muscle sling within the Pomacentridae is found to characterize groups congruent with those characterized by other characters, a case could be made for suggesting the muscle sling developed within that clade. If, alternatively, the presence of a muscle sling is in conflict with the distribution of other characters and the absence characterizes corroborated groupings, absence could be considered as the derived condition. Lacking a precise knowledge of the intrarelationship of pomacentrid clades and based on the absence of a muscle sling in other pharyngognathous perciforms, we tentatively favor the second alternative and suggest that the muscle sling is indeed primitive for the Labroidei. However, we freely acknowledge that this is a relatively weak assumption and that future work may support alternative interpretations.

A remarkable similarity exists between the labroid muscle sling and that of exocoetid beloniforms (compare Figs. 2E and 9A or B). In the latter group the le4 (and a small slip of the levator posterior muscle) merges with a division of the obliquus posterior and inserts onto the LPJ, thus morphologically (and presumably also functionally) simulating the labroid configuration in remarkable detail. A similar muscle sling is not developed in the scomberesocids (Fig. 2D), and in these taxa a well-developed obliquus posterior and a fifth adductor connect the LPJ with the dorsal elements. The le4 and levator posterior both insert onto the head of the fourth epibranchial, and no fibers pass below it.

Quite apart from the striking suite of (homoplastic) morphological similarities

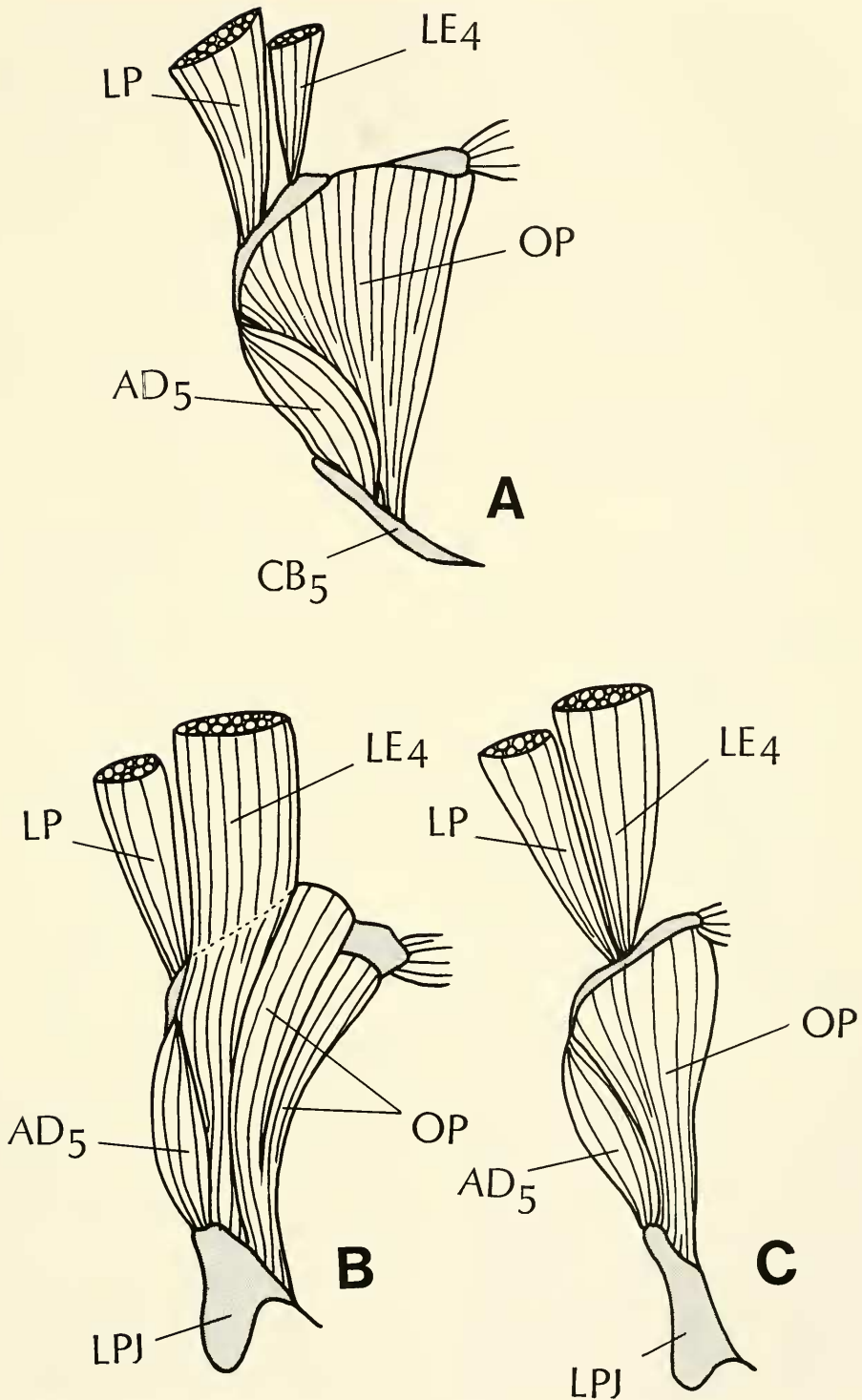


Figure 8. Isolated pharyngeal "muscle sling" components in: A. *Percichthys*; B. *Stegastes*; C. *Chromis*.

between the PJAs of exocoetids and labroids, these two lineages (as well as the scomberesocids) differ from other taxa in that *all* members possess the pharyngognathous condition of functionally united fifth ceratobranchials, regardless of the diet of each species. In other families the expression of pharyngognathy is limited to only a few (presumably duraphagous) members of each lineage, and is repeatedly correlated with an overall pharyngeal hypertrophy. The labroid pharyngeal synapomorphies (and the similar, but independently derived, beloniform ones) are not simply correlated with a durophagous diet; these taxa bear the synapomorphies regardless of the particulars of diet and trophic modification peculiar to individual species.

As indicated by the above discussion, the possession of united fifth ceratobranchials, i.e., pharyngognathy, is actually quite mosaically distributed among perciforms and at this level at least, is not indicative of any close phylogenetic relationship between the taxa in which it occurs. Thus, although it was originally in this context that the taxa comprising the Labroidei were considered to be closely related, the shared possession of the pharyngognathous condition is not itself the most compelling evidence for the monophyly of this clade. However, the fact that *all* labroid taxa, with the exception of *Cichla* (Stiassny, 1982), express united fifth ceratobranchials does suggest that this feature may have some value in uniting the Labroidei. While it is true that most labroids have a hypertrophied PJA capable of a powerful pharyngeal bite (Liem and Greenwood, 1981), this is by no means universal within the clade (e.g., Emery, 1973; Stiassny, 1982; Yamaoka, 1978). Nevertheless, even those labroids with extremely weak pharyngeal development exhibit the pharyngognathous condition of fused fifth ceratobranchials. Such universality of pharyngognathy, in the face of considerable pharyngeal variation, is unique among perciforms, and we consid-

er this to be an indication that structural and functional union of the fifth ceratobranchials is primitive for the Labroidei and that its presence in forms with poor pharyngeal development merely reflects a retention of the primitive condition.

The Labroidei can thus be diagnosed on the basis of the presence of the following configuration of the pharyngeal jaw apparatus:

1. A LPJ with a well-developed ventral keel, onto which is inserted a portion of the transversus ventralis IV muscle.
2. A true diarthrosis between the UPJ and neurocranial apophysis.
3. A neurocranial apophysis of characteristic ventrally projecting and rounded form.
4. Presence of a m. transversus pharyngobranchialis 2 division of the transversus anterior muscle complex (secondarily reduced in the Embiotocidae). This character is somewhat ambiguous (see discussion on page 276).
5. An undivided sphincter oesophagi muscle.
6. A muscle sling directly suspending the LPJ from the neurocranium (polymorphically expressed within the Pomacentridae). See page 284 for a discussion of this character.
7. A structural union of the LPJ even in the absence of pharyngeal hypertrophy and functional duraphagy.

The interesting preponderance of characters concerning the pharyngeal jaw apparatus in labroid systematics is discussed further on pages 306–308. In the course of this investigation a further character of the pharyngeal region (although not obviously functionally related to the PJA) has been identified, and before concluding this section on labroid monophyly that character is discussed.

As already noted, extensive data exist on the configuration of dorsal branchial arch elements in acanthomorph fishes, but considerably less is known about variation in the ventral branchial elements. Fortu-

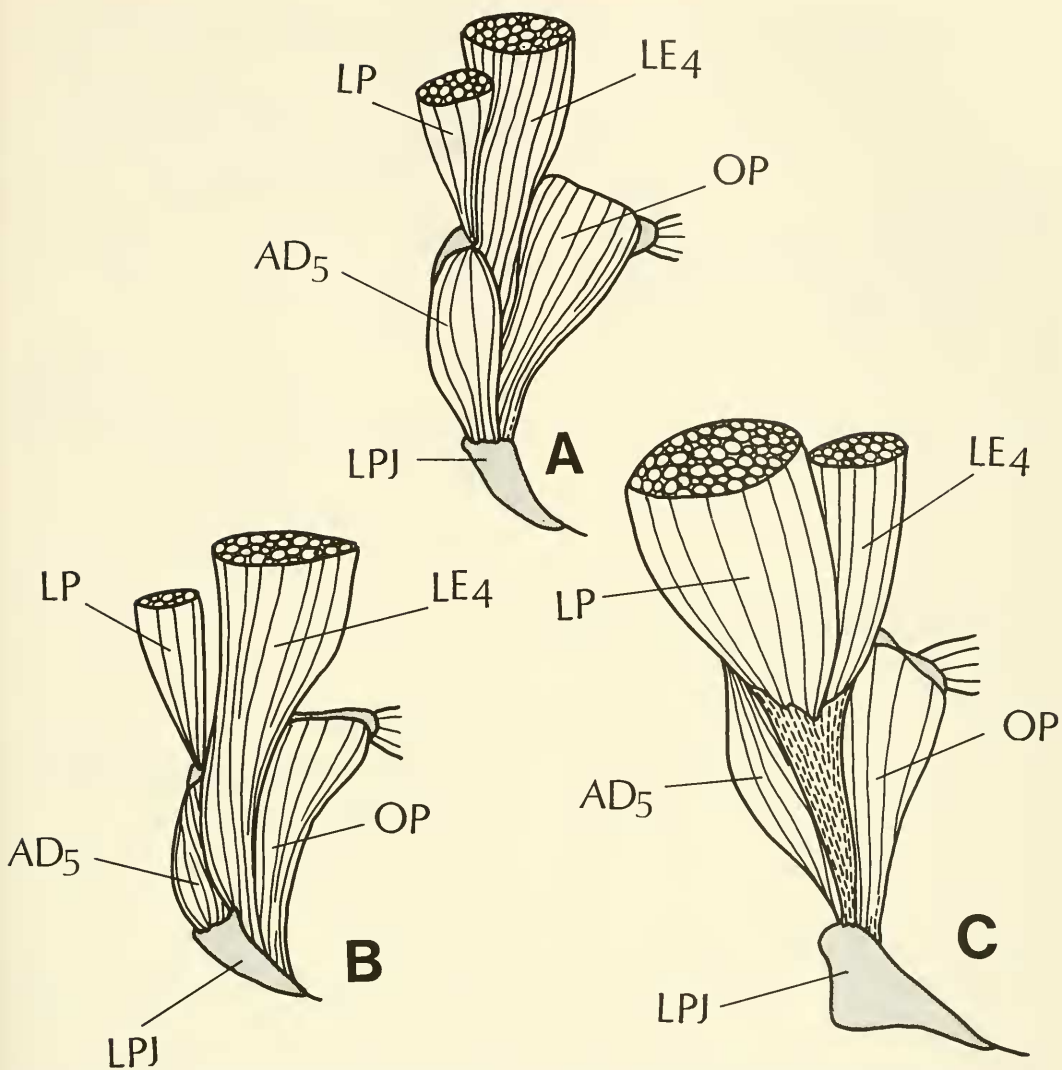


Figure 9. Isolated pharyngeal "muscle sling" components in: A. *Astatotilapia*; B. *Ditrema*; C. *Labrus*.

nately some comparative data are available (e.g., Nelson, 1967a, 1969; Travers, 1984a,b). Investigation of the configuration and associations of the ventral branchial arch elements of labroid fishes renders several features that may be potentially useful in resolving labroid intrarelations (page 296).

In addition to these features, a particular configuration of basibranchial elements characterizes the entire Labroidei.

In labroids the first basibranchial is an elongate, cylindrical element situated partially below the axis of the basihyal and the remaining elements of the basibranchial series (Figs. 10A–E). Although there is considerable variation in this osteological complex, the first basibranchial does not lie below the axis of the basihyal and remaining elements in the majority of outgroup taxa examined. In most outgroup taxa, rather, the first basibranchial is a lat-

erally compressed, almost square element and the basihyal/basibranchial series are more or less horizontally aligned with the first basibranchial abutting the caudal margin of the basihyal element (Fig. 10D; Nelson, 1967a, 1969; Travers, 1984a,b). Among outgroups a similar configuration was found only in the girellid, *Girella*.

In view of its limited distribution, the presence of an elongate, cylindrical first basibranchial element ventrorostrally displaced to lie partially below the basihyal axis is interpreted as an additional synapomorphy uniting the labroid clade, and the presence of similar modifications in *Girella* is presumed to be homoplasous.

In summary, the monophyly of the Labroidei seems to have been established beyond any reasonable doubt. Seven of the eight characters used in the definition of the assemblage are features of the pharyngeal jaw apparatus, and the eighth (i.e., the basibranchial character described above), although not obviously implicated in the PJA, is also a character of the pharyngeal region. Despite a conscious and concerted effort to locate synapomorphies in other structural (functional) systems, the weight of evidence for labroid monophyly remains in the pharynx (see discussion on pages 306–308).

LABROID INTRARELATIONSHIPS

CHARACTER SURVEY

In this section we review the various characters that have been used in previous analyses of labroid intrarelationships, and present novel data. For ease of description, the characters are arranged into rather loosely defined morphological units wherever possible; otherwise they are simply listed independently. Where appropriate each character or character complex is introduced with a short review of the relevant comparative literature and any problems surrounding past usage of terms or identification of homologies are discussed. As in the preceding section, summary statements of characters as-

essed to be synapomorphic for labroid clades are italicized for ease of reference.

Characters of the Pharyngeal Jaw Apparatus

LPJ Union and Medial Tooth Implantation. As we mentioned, within the Labroidei two modes of LPJ union are expressed. In cichlids the two fifth ceratobranchial elements are united medially in a caudally convoluted and interdigitating suture (Fig. 3B), and the pharyngeal teeth on the corresponding toothplate can be divided into left and right regions with no teeth located over the symphysis of the two bones. Regarding the retention of a sutural union, and the tooth implantation pattern, we agree with Kaufman and Liem (1982) that the cichlid arrangement represents the plesiomorphic labroid condition. In contrast, the condition in adult labrids, pomacentrids and embiotocids is a complete fusion of the two LPJ elements and no trace of the central suture remains (Figs. 3A, C, D). Tooth rows are arranged radially across the LPJ, and teeth are located over the median region of the jaw (Kaufman and Liem, 1982).

Because a similarly derived arrangement is found nowhere else among pharyngognath percomorphs, contrary to Kaufman and Liem (1982), we interpret *the total obliteration of all traces of a sutural union of the two fifth ceratobranchial elements of the LPJ and the implantation of pharyngeal teeth over the midline of the bone to be synapomorphies uniting the labrid embiotocid and pomacentrid radiations.*

Pharyngo-Cleithral Joint. Liem and Greenwood (1981), and later Kaufman and Liem (1982) described what they termed “pharyngo-cleithral joints” in labrid and pomacentrid taxa. The latter authors were of the opinion that the joints in these two lineages are “clearly dissimilar in form” but offer little in the way of substantiation of the claim. The pharyngo-cleithral joint is listed as one of the synapomorphies

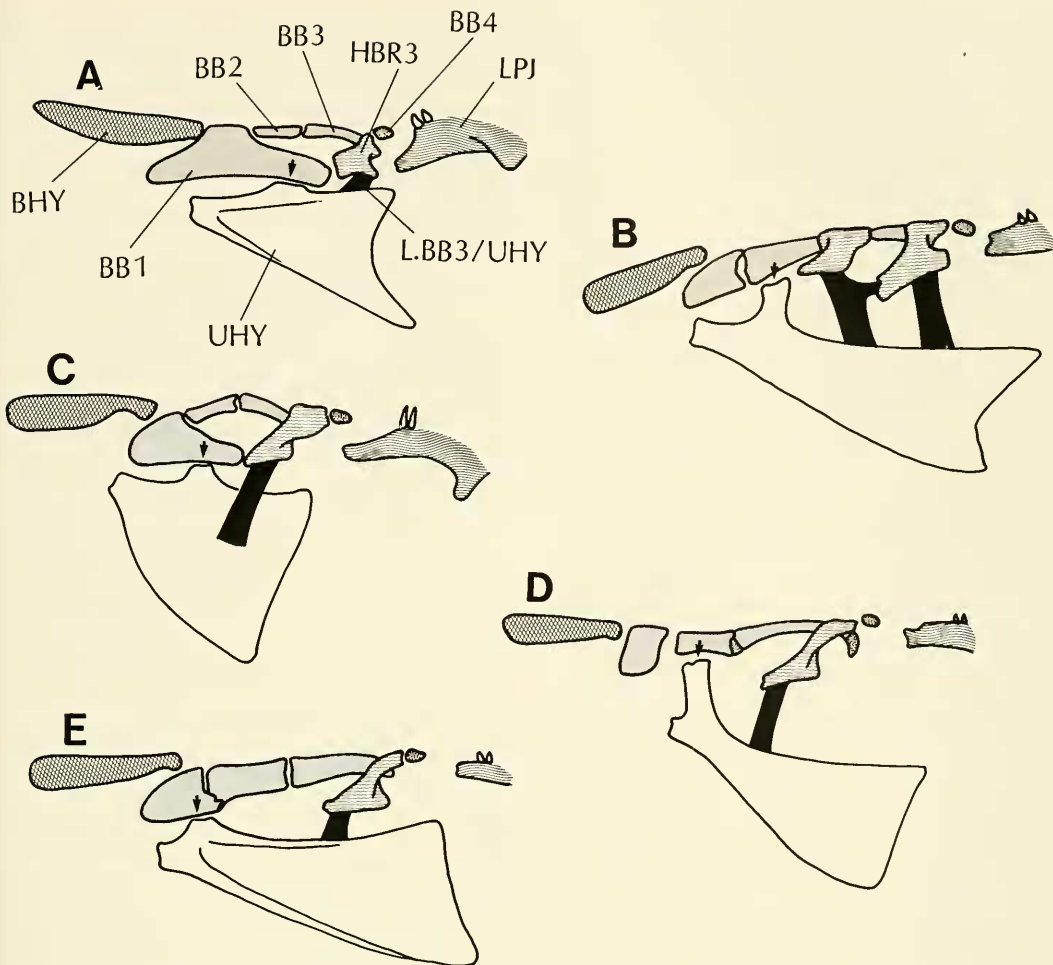


Figure 10. Ventral branchial arch elements in: A. *Labrus*; B. *Astatotilapia*; C. *Pomacentrus*; D. *Percichthys*; E. *Embiotoca* in lateral view.

characterizing the Labridae (Kaufman and Liem, 1982: 9), and Liem and Sanderson (1986) investigated the function of the joint during pharyngeal mastication. Lauder and Liem (1983: 169) cited the presence of a "pharyngo-cleithral articulation of characteristic form" as a synapomorphy of the Pomacentridae. Our observations of the pharyngeal-cleithral associations in various pomacentrid (Fig. 11A) and labrid (Figs. 11B, C) taxa are somewhat at odds with those of these previous investigators and lead to a different con-

clusion regarding the phylogenetic significance of the structural complex.

Among pomacentrids there is considerable variation in the degree to which the expanded lateral horn of the LPJ (=muscular process of Liem, 1973) contacts the cleithrum. In some taxa (e.g., species of *Microspathodon* and *Chromis*) there is no contact and a pharyngo-cleithral articulation is consequently lacking. In others (e.g., species of *Stegastes* and *Pomacentrus*) the area of contact is extensive and similar to that of many labrids.

Among labrids also there is considerable variation in the degree of pharyngo-cleithral contact and, although contact is always established (even in those forms with greatly reduced PJAs), the actual articulation surface may be extremely small (e.g., Fig. 11C). A distinct articular process (fossa?) on the cleithrum, and the consequent development of a true synovial joint (Liem and Greenwood, 1981) are not present in all labrids; in fact the development of such a joint appears to be present only in scarids and odacids (Kaufman and Liem, 1982: fig. 6). In our opinion the morphological differences between labrid (possibly excluding scarids and odacids) and pomacentrid pharyngo-cleithral articulations are quantitative and not qualitative as implied by Kaufman and Liem (1982). What is strikingly similar in these two taxa, however, is the form of the LPJ.

LPJ Form. Representative labroid LPJs are illustrated in Figure 3. Within each of the labroid families there exists a considerable range in both the relative size and shape of the LPJ. This is perhaps least marked in pomacentrids (Emery, 1973) and embiotocids (De Martini, 1969), but in labrids (Gomon and Paxton, 1986; Yamaoka, 1978) and cichlids (Fryer and Iles, 1972; Pellegrin, 1903) the range is truly remarkable. Despite intralineal variation and a number of autapomorphic features (Stiassny, 1980), the labrid and pomacentrid LPJs all share a markedly similar facies. These similarities are rather difficult to quantify precisely; however, they are easily appreciated by a comparison of each of the jaws illustrated in Figure 3. *The labrid/pomacentrid jaw is highly characteristic in being almost Y-shaped, rather than essentially triangular, with an emphasis upon the long lateral horns that are distally expanded. Uniquely in labrids and pomacentrids, LPJ width is greater than (rarely equal to) the LPJ length; this relation is reversed in other taxa. The elongation of the LPJ lateral horns and their distal expansion are synapomorphic features of the labrid and*

pomacentrid LPJ; they are also a structural prerequisite for the development of a pharyngo-cleithral association. As pointed out above, although not strictly a character for use in our analysis, the development of a pharyngo-cleithral articulation in labrids, and its tendency for expression in the pomacentrids, is clearly correlated with these LPJ specializations.

LPJ Muscle Sling. Liem and Greenwood (1981) distinguished between a cichlid/embiotocid type of muscle sling on the one hand and a labrid type on the other. In the former, the fourth levator externus muscle is morphologically and functionally dominant during pharyngeal mastication, while in the Labridae it is the levator posterior muscle that is the dominant element (see also Liem, 1986; Liem and Sanderson, 1986; Yamaoka, 1978). Dominance of the fourth levator is considered by Liem and Greenwood (1981) to be part of a unique, specialized complex characterizing the Cichlidae-Embiotocidae lineage, while dominance of the levator posterior, forming a force couple with the pharyngocleithralis externus muscle, is considered by Kaufman and Liem (1982) to be one of the synapomorphies characterizing the Labridae.

It seems most probable that a structural and functional dominance of the fourth levator is the primitive condition of the labroid muscle sling for two reasons: in Pomacentrids the levator posterior never contributes to the muscle sling, and in outgroup taxa the levator posterior is invariably smaller and less well-developed than the fourth levator externus. The highly complex and elaborate muscular sling of the Labridae (Kaufman and Liem, 1982; Liem and Sanderson, 1986) is correctly interpreted as an autapomorphy of that clade.

Stiassny (1980) proposed that a caudad migration of the levator posterior origin away from the "lateral awning" (Barel *et al.*, 1976) on the ventral face of the pterotic or intercalar bone is a synapomorphy uniting the Embiotocidae and Labridae.

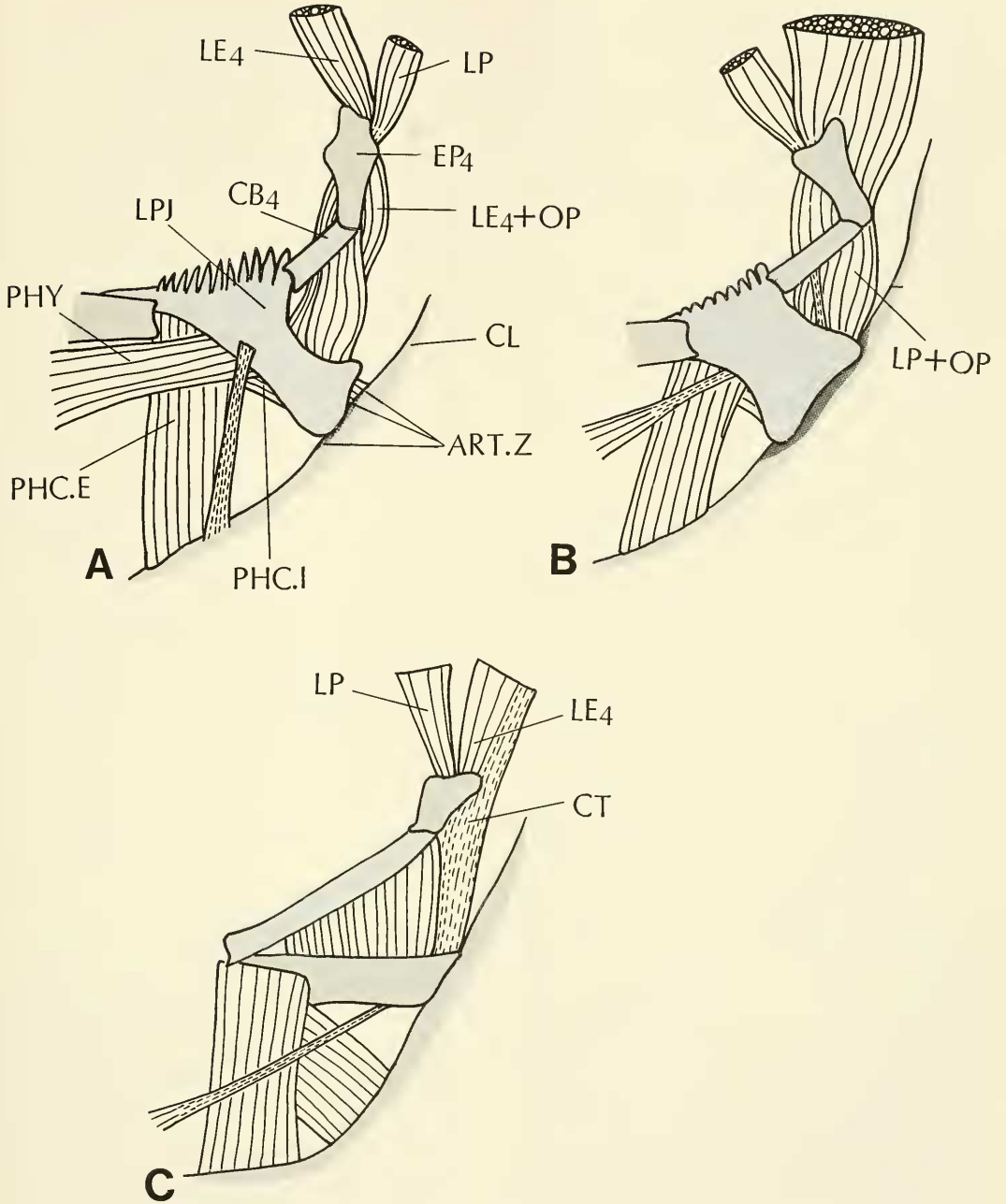


Figure 11. Pharyngo-cleithral associations in: A. *Eupomacentrus*; B. *Labrus*; C. *Labroides dimidiatus*.

Our reinvestigation of this character fails to reveal any significant differences between the location of levator insertion sites in pomacentrids, cichlids and embiotocids. Within the Labridae an extremely wide range of sites are encountered and based upon these Yamaoka (1978) has constructed a morpho-ecological classification of labrid types.

UPJ Composition. The structure of the dorsal gill arches has figured prominently in studies of euteleostean relationships (e.g., Nelson, 1969; Rosen, 1973), and a number of dorsal gill arch characters have direct bearing on relationships within the Labroidei (Kaufman and Liem, 1982; Liem and Greenwood, 1981; Nelson, 1967a; Stiassny, 1980, 1981). A summary of plesiomorphous osteological and myological features of the perciform upper pharynx is given by Stiassny (1981, 1982).

Upper Pharyngeal Toothplates. Compared with the modal perciform arrangement (Stiassny, 1981), within the Labroidei reduction of a number of features of dorsal gill arch osteology is evident. *In the Embiotocidae (Figs. 12B, 13B) and Labridae (Fig. 12D) the second pharyngobranchial is reduced to a slender, rod-like element with no trace of a second pharyngobranchial toothplate* (Nelson, 1967a). This condition stands in contrast to that seen in the Cichlidae (Fig. 12A), the Pomacentridae (Fig. 12C), and the majority of outgroups, in which the second pharyngobranchials are robust elements each bearing a well-developed toothplate.

Loss of the second pharyngobranchial toothplates occurs elsewhere within the Percomorpha, most notably among the Blenniidae (Springer, 1968), in which the entire second pharyngobranchial is absent and only a single toothbearing element (pharyngobranchial 3 and 4?) is present. In a single mastacembelid lineage the second pharyngobranchial is reduced to a small cartilage (Travers, 1984b). Despite the occasional loss of the second pharyngobranchial toothplate elsewhere within the Percomorpha (Stiassny, 1981), we

consider the absence of this structure in the Embiotocidae and Labridae to be evidence suggestive of a sistergroup relationship between them.

As in the Euteleostei generally, the paired third pharyngobranchial elements (and associated toothplates) comprise the major component of the upper pharyngeal jaw in labroids (Nelson, 1967a, 1969). In the Cichlidae (Fig. 12A) and Pomacentridae (Fig. 12C) the fourth upper toothplates also contribute significantly to the composition of the UPJ, and are suturally united to their respective third pharyngobranchials. Typically among outgroup taxa the fourth upper toothplate is well-developed and cups around a cartilaginous fourth pharyngobranchial, although rarely it is as intimately associated with the third pharyngobranchial or as highly ossified as in cichlids and pomacentrids (Stiassny, 1981).

In embiotocids Up4 is a fragile, weakly ossified element with feebly developed teeth and relatively little common border with its associated third pharyngobranchial (Fig. 12B). In the Labridae no evidence remains of an independent Up4 (Fig. 12D; see also Nelson, 1967a, 1969). *We consider the reduction of the Up4 element in the upper pharyngeal jaw to be a synapomorphy of these two labroid taxa.* Ontogenetic data may clarify the nature of the reduction of this character within the Labridae.

The families Cichlidae and Embiotocidae share a cartilaginous cap on the anterior border of the second epibranchial (Fig. 14) (Stiassny, 1981). However, reinvestigation of this character leads us to consider this condition non-homologous between the two families. Within the Cichlidae, the second epibranchials bear an expansion rostrally with a cartilaginous cap. This cartilaginous flange does not articulate with any other pharyngeal element, and extends forward into the buccal cavity forming the core of pharyngeal pad developed on the mouth roof (Trewavas, 1973). In addition, the head of the epi-

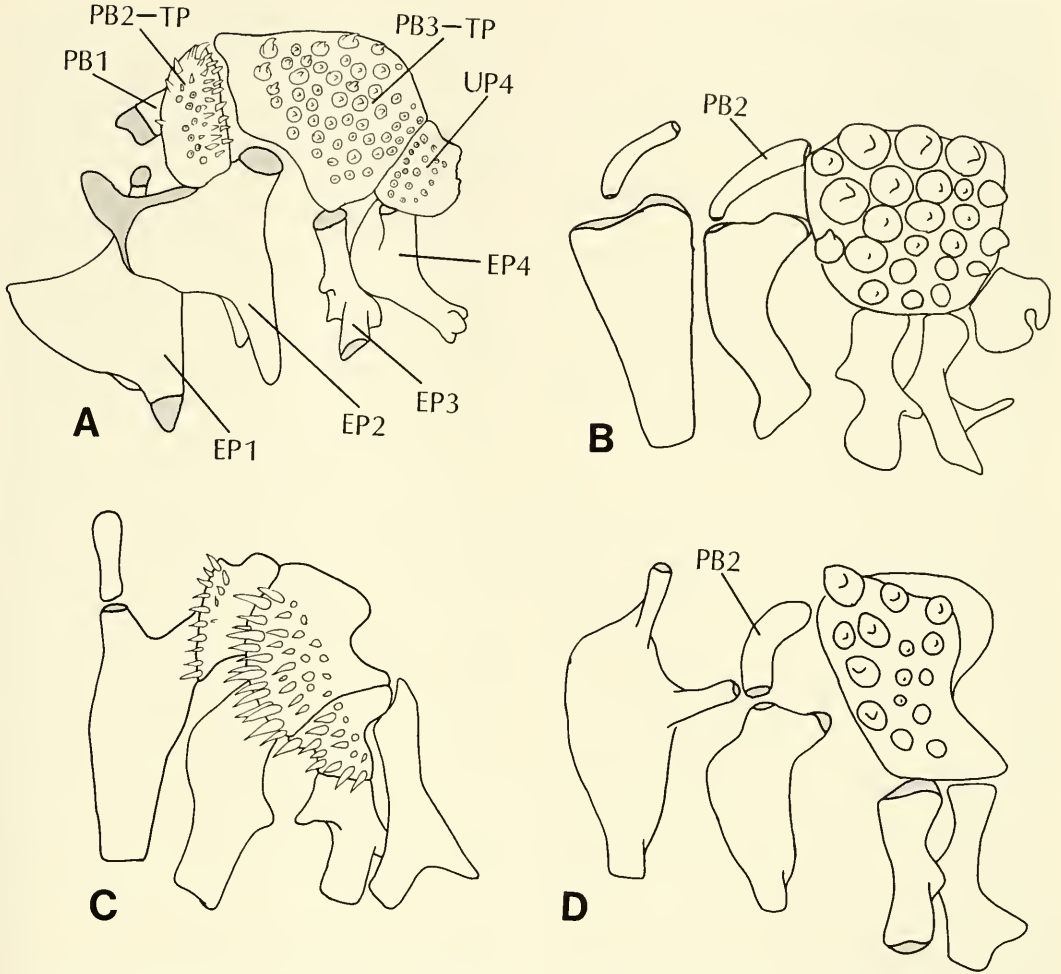


Figure 12. Right upper pharyngeal jaw in ventral view. A. *Geophagus*; B. *Micrometrus*; C. *Stegastes*; D. *Labrus*.

branchial bears two other cartilaginous pads, corresponding to its points of articulation with pharyngobranchials 2 and 3 (Fig. 14A). Within the Embiotocidae, only those cartilaginous pads associated with the pharyngobranchial articulations are present (Fig. 14B), either continuous with each other or separated by a narrow gap. Because the cartilaginous extension on the anterior border of the second epibranchial has no counterpart in the Embiotocidae, in terms of either form or topographic relationship to the adjacent elements, we do not consider this similarity to be indica-

tive of a close relationship between the two families.

Interarcual Cartilage Development. The presence of a cylindrical rod-like interarcual cartilage connecting the uncinate process of the first epibranchial element with a dorsal process of the second pharyngobranchial is considered by Rosen and Greenwood (1976) to be a synapomorphy uniting the Perciformes. In a subsequent review of the morphology and distribution of this structure Travers (1981) concluded that an interarcual cartilage (of some form) is primitively present in a wide

range of ctenosquamate taxa (see also Rosen, 1985).

Among outgroup taxa investigated here a rod-like interarcual cartilage is typically present. Although a well-developed interarcual cartilage is present in most sciaenid and gerreid taxa examined, an interarcual cartilage is lacking in both pharyngognaths *Pogonias cromis* and *Gerres poeiti*. Within the Perciformes the interarcual cartilage has apparently been lost independently a number of times (e.g., Springer, 1968; Travers 1981, 1984a). Johnson (1984) listed the presence or absence of an interarcual cartilage in representatives of all percoid families.

Within the Labroidei, a rod-like interarcual cartilage is fully developed in the Pomacentridae (Fig. 13C), reduced or absent among the Cichlidae (Fig. 13A; see also Stiassny, 1981), and completely absent in both the Labridae (Fig. 13D) and Embiotocidae (Fig. 13B). The cichlid condition is complex as an interarcual (present as a nubble of cartilage suspended in a connective tissue strand) occurs in many Neotropical and Madagascan lineages but is present only very rarely as an individual anomaly in the more derived African lineage (Stiassny, in press). As the Cichlidae is polymorphic for this character we tentatively consider the cartilage to be primitively present, but reduced in the family, perhaps having been lost independently several times within the clade. *The complete absence of an interarcual cartilage is interpreted as a synapomorphy of the Labridae and Embiotocidae.*

Stiassny (1980) cited the loss of a well-developed anterodorsal process on the second pharyngobranchial (primitively accommodating the medial end of the interarcual cartilage) as a synapomorphy uniting the Labridae, Embiotocidae and Cichlidae. Reexamination of this character fails to corroborate that assessment. Comparison of second pharyngobranchial morphology in a range of cichlid and pomacentrid and additional outgroup taxa does not reveal any significant difference

in the degree of development of this process in these taxa. The fact that the process is lacking on the second pharyngobranchials of labrids and embiotocids is clearly related to the overall reduction of the elements in these taxa.

With regard to branchial osteology, the monotypic family Pholidichthyidae mirrors the Labridae (and in some respects other labroids also) to a remarkable extent. *Pholidichthys* lacks a cartilaginous fourth pharyngobranchial, a fourth upper toothplate, epibranchials 3 and 4 articulate with the third pharyngobranchial, no interarcual cartilage is present and the second pharyngobranchial lacks a toothplate and anterodorsal process (Springer and Freihofer, 1976). In addition the fifth ceratobranchials of *Pholidichthys* are also united into a single element. Unfortunately no specimens of this genus were available to us for dissection so we are unable to comment on the condition of the branchial myology of these fishes. An investigation of their myological configuration is particularly interesting with regard to the possible development of a pharyngeal muscle sling in these taxa. (See discussion of beloniform/labroid pharyngeal parallels on pages 274–286.)

Additional Characters of the Pharyngeal Region

Ventral Branchial Myology. In a phylogenetic context, teleostean ventral branchial myology has received far less attention than the corresponding dorsal configuration. Although much information is available in papers describing the myology of various individual taxa, few comparative data have been assembled with a view to resolving problems of phylogenetic relationship. The works of Dietz (1921), Nelson (1967b), Winterbottom (1974) and Lauder (1983) are notable exceptions and provided much valuable comparative information. Goedel (1974a,b) and Anker (1978) also provided useful data on the ventral branchial mus-

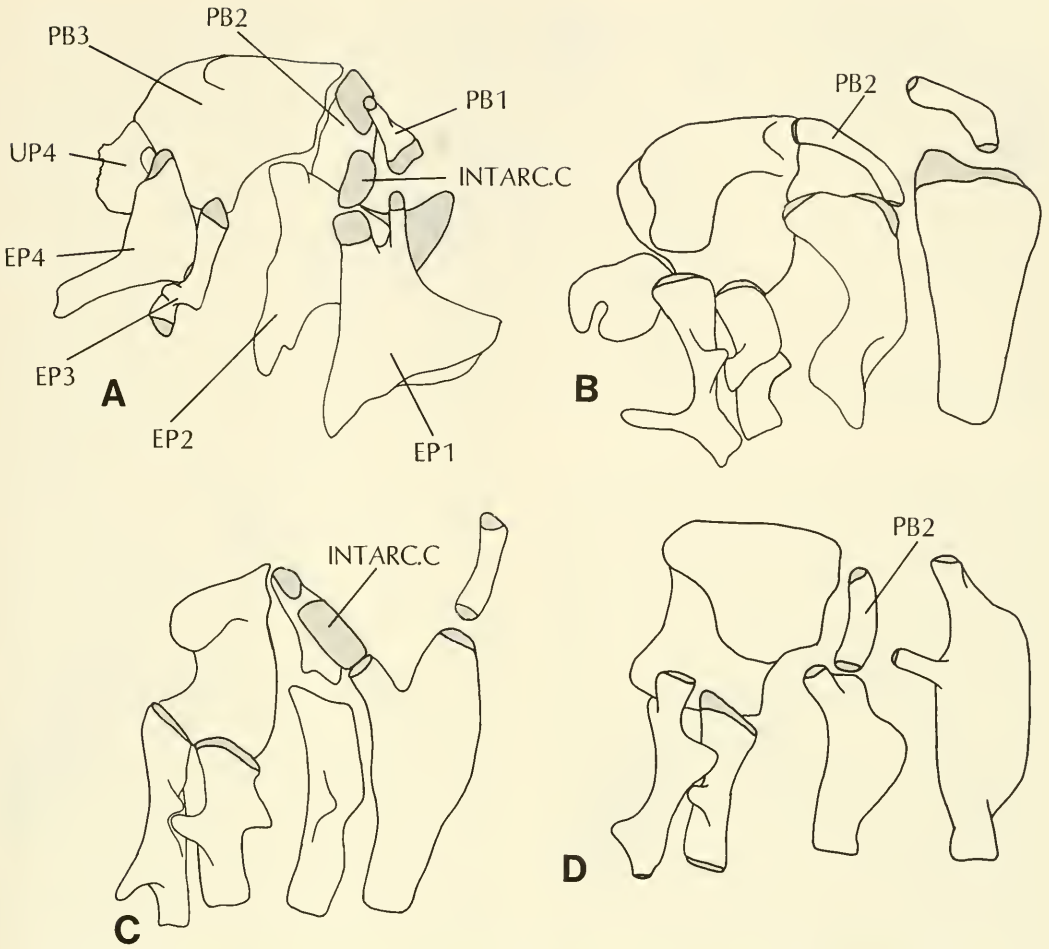


Figure 13. Right upper pharyngeal jaw in dorsal view. A. *Geophagus*; B. *Micrometrus*; C. *Stegastes*; D. *Labrus*.

cles of two African cichlid fishes, and characters of the ventral branchial musculature of labroids are employed by Stiassny (1982, and in press) and Greenwood (1985).

The plesiomorphic perciform configuration of ventral branchial muscles is represented here by the arrangement in *Morone* (Fig. 4A). Both the *rectus ventralis IV* and *obliquus ventralis IV* insert together onto a well-developed semicircular ligament system. Among labroids a similar configuration is present in embiotocids (Fig. 4B) and most cichlids (Fig. 4C; Greenwood, 1985 and Stiassny, in press),

as well as in the percoid outgroups examined (*Serranus* lacks the semicircular ligament system entirely [Stiassny, in press]).

In labrids (Fig. 4D) and pomacentrids (Fig. 4E) the *rectus IV* and *obliquus IV* muscles insert independently on the semicircular ligament. Although a seemingly minor distinction, these insertional differences consistently appear to differentiate labrids and pomacentrids from the other perciform taxa examined, and as such are interpreted as synapomorphic for the two lineages.

Primitively among acanthomorphs a

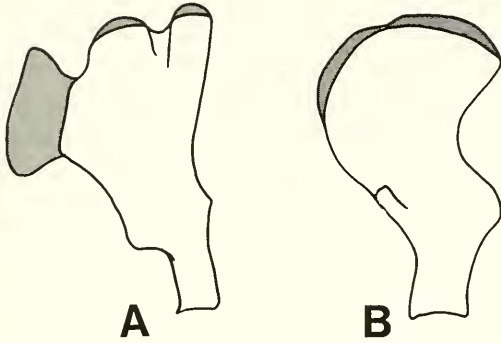


Figure 14. Isolated second epibranchial element. A. *Astatotilapia*; B. *Cymatogaster*.

single ligament passes from the third hypobranchial element of either side to attach to the dorsal surface of the urohyal (ligamentum urohyale caudale of Anker, 1978). Uniquely in the Cichlidae (Fig. 10B) an additional ligament (ligamentum urohyale intermedium of Anker, 1978) passes from the second hypobranchial element of either side to attach to the dorsal surface of the urohyal somewhat in advance of the caudal ligament. A similar elaboration of a ventral branchial ligament system is lacking in all other taxa and is identified as an additional synapomorphy uniting the members of the Cichlidae.

Ventral Branchial Osteology. There exists a large body of data on the configuration of dorsal branchial osteology, but as with the myology of the region, less is known of the variation in the ventral branchial elements. Some comparative data are available (e.g., Nelson, 1967a, 1969; Travers, 1984a,b) and these provide useful additional outgroup data.

In labrid (Fig. 10A), pomacentrid (Fig. 10C) and embiotocid (Fig. 10E) taxa the urohyal articulates via its dorsal process with the ventral surface of the first basibranchial element. This is not the case in cichlids (Fig. 10B), nor in the majority of percoid outgroups examined (e.g., Fig. 10D) where the urohyal articulates with the second basibranchial (occasionally at

the cartilaginous junction of the first and second basibranchials).

Gerres and *Eucinostomus* provide exceptions to the above generalization and in these taxa the urohyal (although lacking a distinct dorsal process) articulates directly with basibranchial one. A similar association is present in the majority of Asian (but not African) mastacembelids and synbranchids (Travers, 1984a,b).

Despite these few mosaic occurrences, in the overwhelming majority of acanthomorph taxa the urohyal articulates with the second basibranchial, and the occurrence of a *basibranchial one/urohyal association in labrids, pomacentrids and embiotocids is interpreted as a synapomorphy uniting these three taxa.*

In labrids and pomacentrids (Figs. 10A, C) the urohyal articulates with a large keel-like caudally directed ventral extension developed on the elongate cylindrical first basibranchial element. Primitively among perciforms the first basibranchial is a deep, almost square element that lacks a ventral process (e.g., Fig. 10D). In cichlids and embiotocids the first basibranchial is also somewhat elongate and cylindrical and varies in size. A well-developed caudally directed ventral process, however, is never developed in the manner or extent approaching that of the pomacentrids and labrids.

The mastacembelid and synbranchid lineage described by Travers (1984a,b) prove exceptional among outgroups in the possession of well-developed ventral processes on the first basibranchial.

Despite the occurrence of a similar basibranchial morphology in the labrid/pomacentrid pair and in the distantly related symbranchid/mastacembelid lineage, the labrid/pomacentrid basibranchial configuration is interpreted as a synapomorphy uniting these two taxa.

Caudal Fin Skeleton. Extensive literature exists on the systematic value and distribution of variation in caudal structure within the Acanthomorpha (e.g., Ford, 1937; Gosline, 1961; Hollister, 1936, 1937;

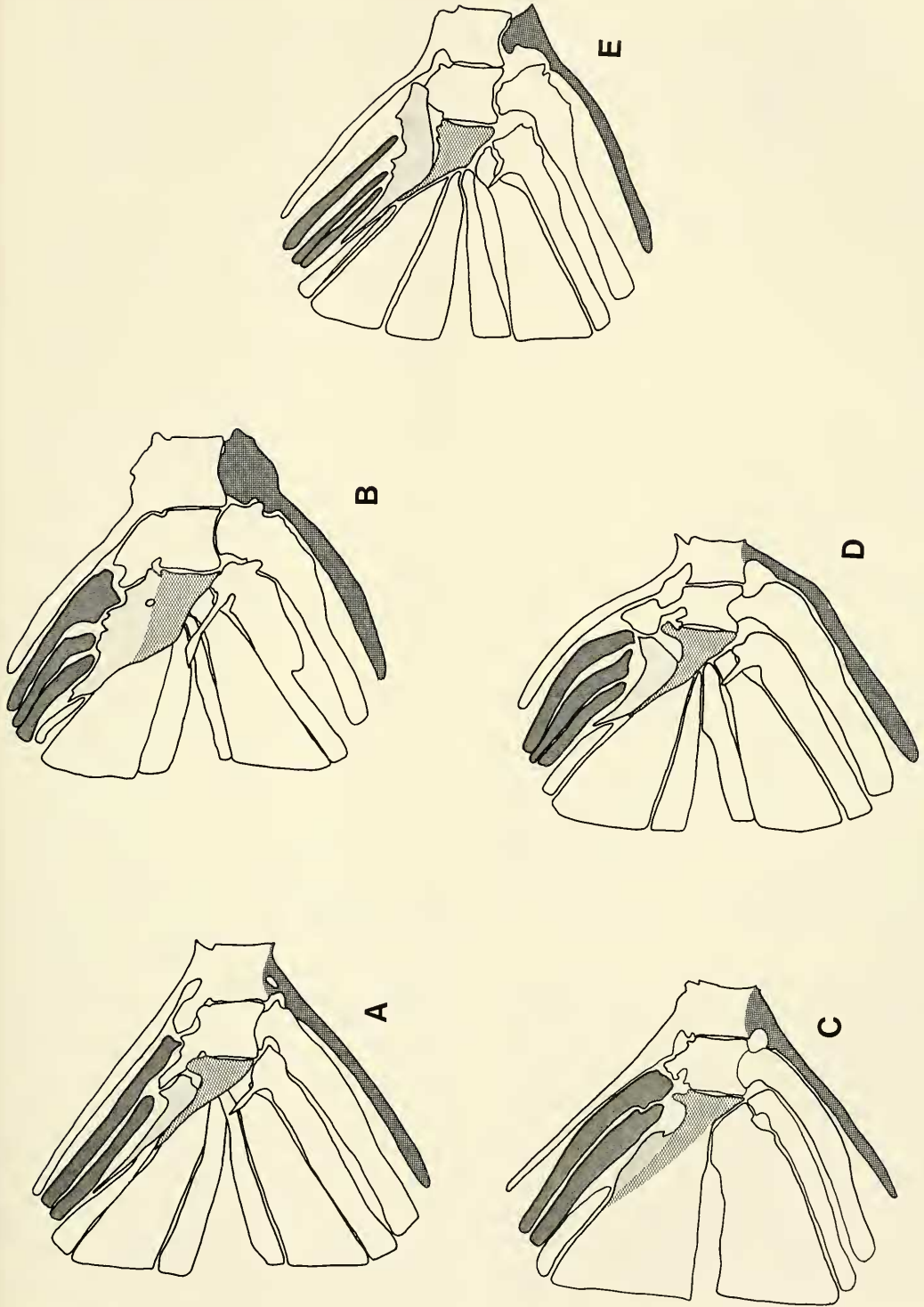


Figure 15. Caudal skeleton of: A. *Cichla*; B. *Stegastes*; C. *Labrus*; D. *Embiotoca*; E. *Percichthys*.

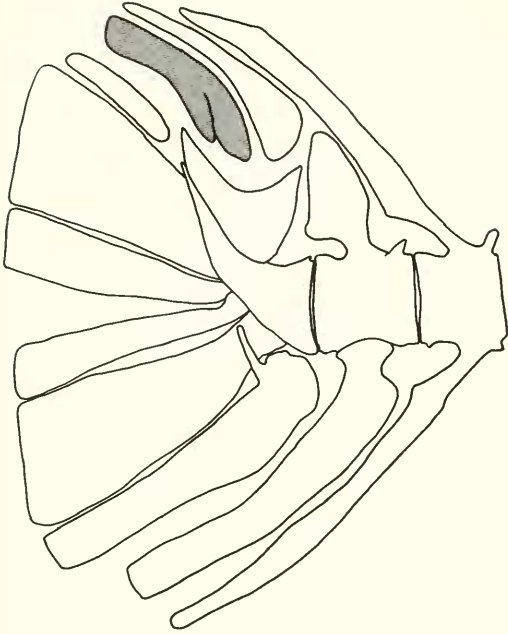


Figure 16. Caudal skeleton of *A. Hysterochrysurus* (40 mm SL).

Johnson, 1984; Patterson, 1968; Rosen, 1973; Rosen and Patterson, 1969). The basal perciform caudal skeleton has been described by Gosline (1961) as having three epurals, two independent uroneural ossifications, and the hemal arches on the penultimate and antepenultimate vertebrae autogenous. Patterson (1968) further characterized the basal Perciform caudal skeleton as having, among other features, a low neural crest on the penultimate vertebrae.

Epural Reduction. In labrid (Fig. 15C; see also Ford, 1937) and cichlid (Fig. 15A; see also Vandewalle, 1973) taxa there are two epural bones in the caudal skeleton. Among perciforms the primitive condition, as found in the Embiotocidae (Fig. 15D), Pomacentridae (Fig. 15B), and most of the outgroup taxa examined (e.g., Fig. 15E), is the possession of three epurals (see also Gosline, 1961). Although exceptional among embiotocids, individuals of *Hysterochrysurus* (Fig. 16) and *Micrometrus* are occasionally found with only two inde-

pendent epurals. In these individuals the anomaly appears to be the result of fusion. In young *Hysterochrysurus*, three separate epurals are present, whereas in the adult these are occasionally united along a portion of their border. The labrids and cichlids bear no trace of a third epural at any time during ontogeny.

Despite the somewhat mosaic distribution of epural reduction among phylogenetically disparate acanthomorph taxa (e.g., reduction occurs in a range of seranid lineages as well as in a number of "paracanthopterygians" [Rosen and Patterson, 1969]), three epurals is undoubtedly the primitive condition for perciforms (Patterson, 1968). In view of this we interpret the reduction of epural number in the Labridae and Cichlidae as a synapomorphy uniting the two clades.

Uroneural Ossification. In common with a range of perciform taxa, the labroid caudal skeleton has but a single uroneural ossification (Gosline, 1961). In the Embiotocidae and Cichlidae, the uroneural is autogenous, as it is in all outgroup taxa examined (e.g., Fig. 15E). Embiotocids differ from outgroups, however, in having the uroneural elements very closely applied to the urostyle (Fig. 15D); nonetheless the uroneural can easily be dissected free of the urostyle without damage to either element. In the Pomacentridae and Labridae the uroneural element is completely fused with the urostyle, resulting in a urostyle/uroneural block with no suture evident between the two elements (e.g., Fig. 15B). In labrids, hypurals 4 and 5 are also fused to the uroneural/urostyle block (Fig. 15C; see also Ford, 1937), a condition we consider to be synapomorphic for members of the Labridae.

Complete fusion of the uroneural with the urostyle, and the obliteration of all trace of a former sutural union, is interpreted as a synapomorphy uniting the pomacentrid and labrid clades.

Antepenultimate Vertebrae. Primitive among perciforms, the hemal arch of

the antepenultimate vertebra remains free from, although very closely associated with, its centrum (e.g., Fig. 15E; see also Gosline, 1961). Among labroids an autogenous hemal arch is also found in the Pomacentridae (Fig. 15B), where the hemal spine of the antepenultimate vertebra articulates with the centrum via a peg-like dorsal extension. The division between the two bones is clearly evident. Embiotocids, cichlids, and labrids exhibit a derived condition in having the hemal spine fused with the antepenultimate vertebra. Even in the early ontogeny of these elements (ca. 10 mm SL), there is no discernible division between these elements.

Although fusion of the antepenultimate centrum and hemal spine occurs in some other acanthomorph taxa (e.g., Gosline, 1961; Hollister, 1937; Springer, 1968), its absence in any of the perciform outgroup taxa examined in the course of our investigation leads us to consider this character as a synapomorphy uniting the labrids, embiotocids and cichlids.

Additional Characters

Subocular Shelf. The presence of a subocular shelf, usually formed by a medial extension of the third suborbital, is widespread among perciforms and appears to have been independently lost a number of times within this taxon (Smith and Bailey, 1962). Among the labroids the Pomacentridae and Embiotocidae have the subocular shelf, whereas the Cichlidae and Labridae do not. The markedly mosaic distribution of this character among outgroups renders polarity determination of the character extremely difficult. For example, a subocular shelf is absent in the Centrarchidae, Kyphosidae, Leiognathidae and Percidae, but is present in the Girellidae, Serranidae, and Sparidae. Even within the Gerreidae, this character is variable (Smith and Bailey, 1962). Clearly the subocular shelf has been lost repeatedly during perciform evolution. In the absence of a clearer knowledge of the precise relationships of the labroids to other

perciform taxa, we are unable to determine the primitive labroid condition.

Endopterygoid Shelf. As noted by Stiassny (1980), primitively among acanthomorphs, the endopterygoid bone of the suspensorium bears a medially directed shelf forming the floor of the orbit. The adductor arcus palatini muscle inserts onto the endopterygoid shelf and, although the extent of adductor migration over the shelf varies (Rosen, 1973), insertion is invariably onto the lateral face of the bone.

In labrids and cichlids the medially directed endopterygoid shelf of other acanthomorphs is lacking, and the adductor arcus palatini inserts onto the medial face of the endopterygoid. The floor of the orbit now lacks a bony component and is instead entirely muscular. In both pomacentrids and embiotocids the endopterygoid shelf is well-developed and adductor insertion is onto its medial face.

Among all of the outgroup taxa investigated an endopterygoid shelf was lacking only in the single species of Mullidae examined. In this taxon the adductor also inserts onto the medial face of the bone and the floor of the orbit is entirely muscular. *In view of the extremely limited distribution of this feature within the Acanthomorpha, we interpret the loss of an endopterygoid shelf, and the subsequent migration of the adductor arcus palatini muscle from the lateral to the medial face of the endopterygoid, to be a synapomorphy of the Cichlidae and Labridae.*

Predorsal Bones. The structure and evolution of the predorsal bones have been extensively reviewed by Smith and Bailey (1961). Predorsals have generally been viewed as representing rayless pterygiophores (Smith and Bailey, 1961); however, it has recently been suggested that they are derived from neural arch material (P. Mabee, personal communication). Whatever their origin, variation in predorsal number is widespread and may be systematically useful at the present level of analysis.

The possession of three predorsal bones is the most common condition among the percoids (Johnson, 1984; Smith and Bailey, 1961) and, judging from the condition seen in most outgroup taxa, is primitive for the Labroidei as well.

Embiotocids and pomacentrids generally retain the primitive number of three predorsal ossifications, whereas the cichlids and labrids display a reduction in predorsal number. *The reduction in predorsal number, to two predorsals in the Labridae and to two or fewer in the Cichlidae, is considered to be a synapomorphy uniting these two families.*

Extrascapular Bones. Among percormorphs the extrascapular series of laterosensory canal bearing ossifications usually overlie the parietal region of the neurocranium. In those taxa in which the epaxial musculature has migrated onto the neurocranium the extrascapulars lie in the dermis superficial to the epaxial musculature (e.g., the Cichlidae). Uniquely among perciforms the extrascapulars have become fused with the parietals of embiotocids and pomacentrids. In these taxa the parietals each bear an open (or partially closed) tube running postero-laterally from the anterior parietal/supraoccipital border (Fig. 6C, D). *In agreement with Morris (1982) we consider the fusion of an extrascapular element with the parietal to be a synapomorphy uniting the Pomacentridae and Embiotocidae.* However, we are unable to corroborate Morris' assertion that a similar extrascapular/parietal fusion also characterizes the Scorpididae. In the representative scorpidid, kyphosid and girellid taxa investigated here, the extrascapular exhibited no particularly close association with the parietal bone of the neurocranium.

Epihemal Ribs. So-called epihemal ribs are developed in some or all representatives of the perciform families Embiotocidae, Pomacentridae, Cichlidae, Scorpididae, Girellidae, Chaetodontidae, Cirrhitidae, and Centrarchidae. Morris (1982) considered the presence of epihemal ribs as an

indication that the pomacentrids (Fig. 17A) and embiotocids (Fig. 17B) bear a closer relationship to each other than either does to cichlids or labrids. However, a review of these structures indicates that the use of the term epihemal rib needs clarification because it describes two morphologically and developmentally distinct structures.

The epihemal ribs of pomacentrids (and scorpidids, girellids, chaetodontids and cirrhitids) are membranous ossifications extending into the horizontal septum between the epaxial and hypaxial musculature, and would thus appear to be modified intermuscular bones. The epihemals of embiotocids (and centrarchids, and a single cichlid species, *Geophagus surinamensis*) appear to be modified pleural ribs. We conclude that the epihemal ribs of embiotocids are distinct from those of pomacentrids, and that they in fact represent pleural ribs, for the following reasons: 1) The epihemal ribs of embiotocids do not extend into the horizontal septum, 2) they are preformed in cartilage as are pleural ribs (but not intermusculars, which are membrane bones and hence are no longer preformed in cartilage (Patterson, 1977)), and 3) the intermusculars and epihemals occur in overlapping series (Fig. 17B; contra Morris, 1982), indicating separate identity.

Although work in progress (Jensen) indicates that the arrangement of epihemal ribs may be informative at the infrafamilial level of analysis, lack of identity between pomacentrid and embiotocid epihemal ribs precludes support for Morris' (1982) statement of relationships based upon these structures. The morphological correspondence between the epihemal ribs of embiotocids and of the single species of cichlid fish is interesting; however, this similarity has little systematic significance.

Maxillary-Palatine Ligament. Stiassny (1980) described a ligament connecting the postmaxillary process of the maxilla with the palatine and ectopterygoid bones of

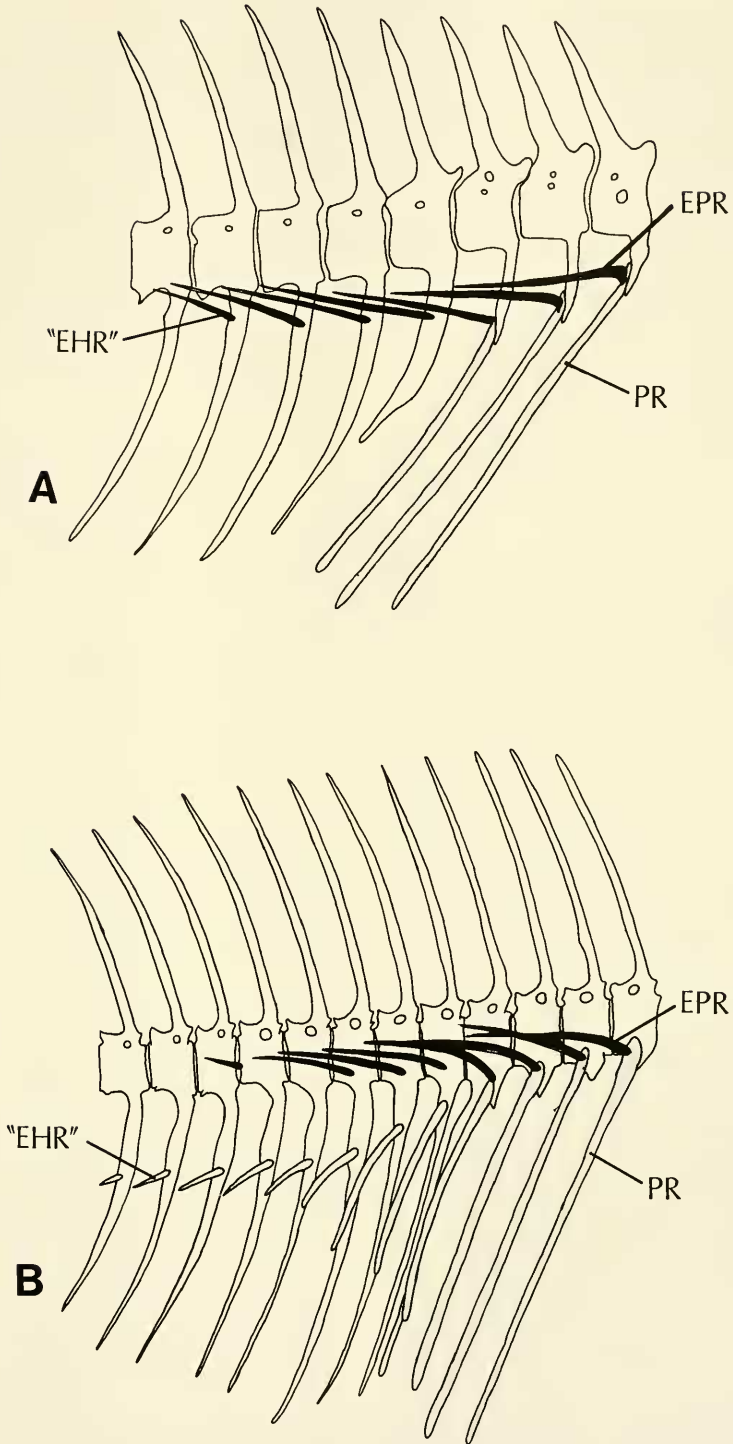


Figure 17. Epihemal ribs in: A. *Eupomacentrus*; B. *Embiotoca*.

the suspensorium as being a synapomorphy uniting the labrid and embiotocid lineages (see also Kaufman and Liem, 1982; Lauder and Liem, 1983). Our reinvestigation of this ligament fails to corroborate that assessment; the degree of development of the ligament varies markedly not only within other labroid taxa (e.g., a range of Neotropical and etropline Cichlidae possess a well-defined and discrete tract of connective tissue connecting the maxillae and palatine/pterygoid region), but also among a range of outgroup taxa examined during the course of this investigation. For this reason the presence of the ligament in labrids and pomacentrids is rejected as evidence of their close relationship.

tA₁ Insertion. Among percomorphs, and neoteleosts in general, control of the maxilla is achieved primarily through an insertion of the A₁ division of the adductor mandibulae muscle onto the posterior border of the maxillo-mandibular ligament, which runs from the lateral face of the maxilla to the lateral face of the angulo-articular (Rosen and Patterson, 1969; Stiassny, 1981). A tendon (tA₁) arising from A₁ and inserting onto the medial face of the maxilla is also primitively present, although usually only weakly developed. Within the Labroidei (and some percoids), there is no association of A₁ with the maxillo-mandibular ligament and maxillary control is primarily through tA₁ (Stiassny, 1980, 1981). The relative insertion sites of tA₁ in cichlids, embiotocids and labrids have been suggested to represent a morphocline of insertion from just below the cranial condyle (cichlids, Fig. 18C), to well onto the cranial condyle (in some embiotocids, Fig. 18A), to a point at the anterior margin of an elongate cranial condyle (labrids, Fig. 18D). The insertion of tA₁ onto the cranial condyle was considered by Stiassny (1980) to be a synapomorphy of an embiotocid-labrid clade. Further investigation of this feature indicates that in fact this character exhibits a continuous range of variation both within and between taxa examined. For example,

the embiotocids span a range of tA₁ insertions (Figs. 18A, B) from that found in cichlids and many other percoids to a condition approaching that of labrids. Within the Cichlidae, in addition, one occasionally finds a condition approaching that of the Labridae (e.g., in the etropline Cichlidae). In view of this, we feel that we would be creating an artificial discontinuity in what is in fact a continuous range of variation if we regarded tA₁ insertion as a synapomorphy of the Embiotocidae and Labridae.

CHARACTER ANALYSIS

Figure 19 depicts the single minimum length tree derived by the PAUP branch and bound routine (Swofford, 1985). This is the shortest tree obtained from the character data (length = 23, consistency index = 0.652) and we favor it with due reservation. The resultant scheme of relationships differs from others previously proposed by Stiassny (1980), Liem and Greenwood (1981), and most recently by Kaufman and Liem (1982), in placing the Cichlidae as the sistergroup of all the remaining labroid groups. The integrity of a monophyletic assemblage composed of the Embiotocidae, Pomacentridae, and Labridae is supported by the presence of three uniquely derived features of the pharynx: the fifth ceratobranchial elements forming the LPJ are completely united such that no trace of a median suture remains, and the pharyngeal tooth rows span radially across the LPJ and overlie the median portion of the jaw (character 1 in Fig. 19); the urohyal articulates via its dorsal process with the first basibranchial element (character 2 in Fig. 19); and the musculus cranio-pharyngobranchialis 2 is absent (character 3 in Fig. 19). The Embiotocidae is placed as the sistergroup of the Pomacentridae plus the Labridae, again in contrast to previous hypotheses of other authors. Four pomacentrid/labrid synapomorphies are identified in a range of structural systems (characters 4, 5, 6, and 7 in Fig. 19).

Although Figure 19 represents the most

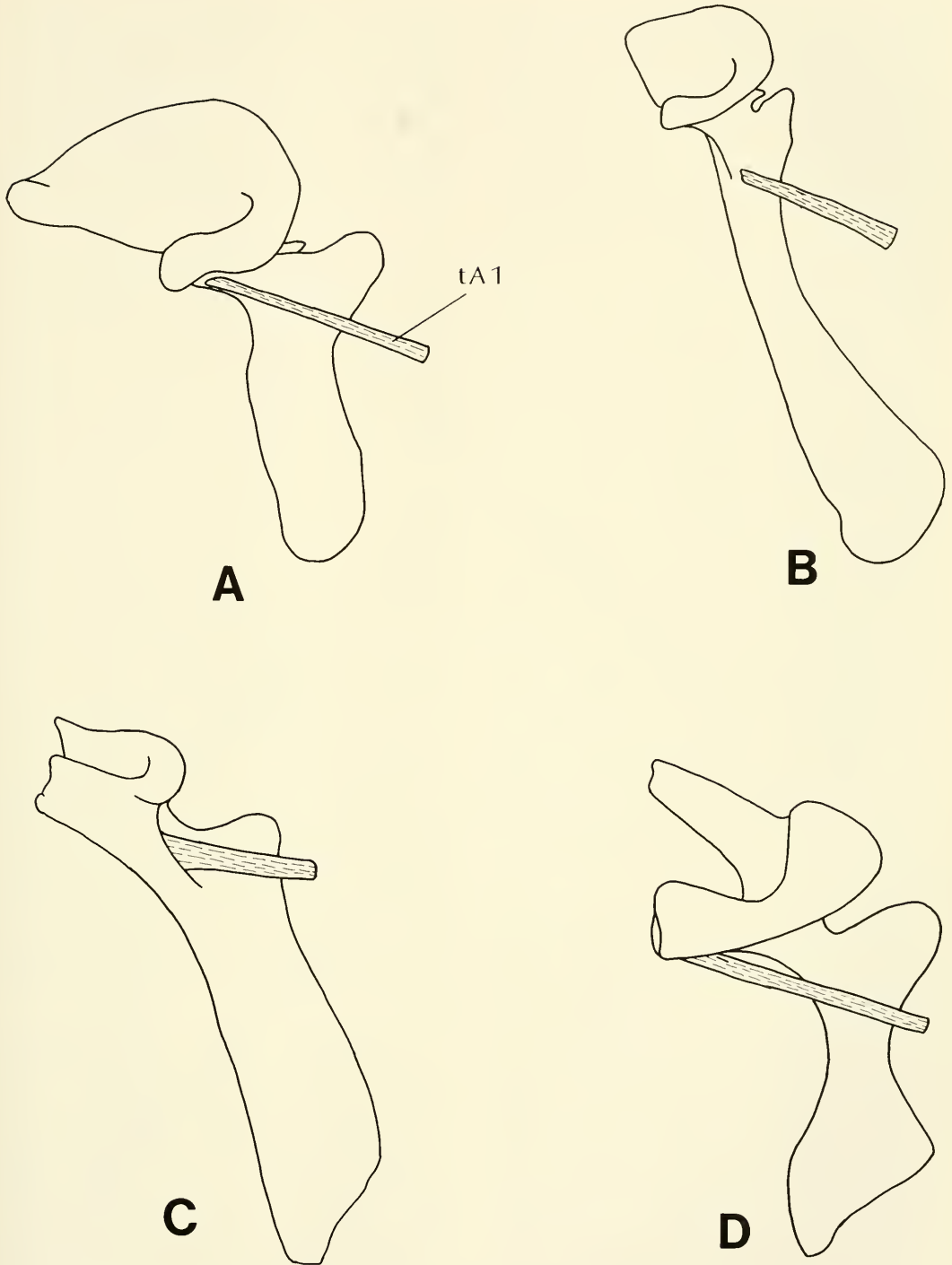


Figure 18. Insertion of tA₁ into the maxilla in: A. *Embiotoca*; B. *Hyperprosopon*; C. *Cichla*; D. *Labrus*.

parsimonious interpretation of the data at hand, the number of crossbars superimposed onto the cladogram starkly illustrates that even this scheme requires the loss or independent gain of many derived characters. Specifically, our hypothesis requires either that the Embiotocidae and Labridae have independently lost the second pharyngeal toothplates and reduced the pharyngobranchial element to a small rod-like structure (character 8), lost the interarcual cartilage (character 10), and have independently reduced (Embiotocidae) and lost (Labridae) the fourth upper toothplate (character 9), or alternatively that the Pomacentridae has undergone a reversal in each of these features. The Cichlidae and Labridae would have to have independently reduced the number of caudal epurals (character 11), reduced the number of predorsals (character 12), and developed an endopterygoid shelf with an (associated) shift in adductor arcus palatini muscle insertion site (character 13). The pomacentrids and embiotocids would have to have independently fused the second extrascapular bone with the parietal (character 14), or alternatively the Labridae would have to have secondarily re-expressed the ancestral condition of this character. Finally, the Pomacentridae would have to have redeveloped an autogenous antepenultimate hemal spine (character 15).

Obviously when dealing with such large amounts of homoplasy a number of alternative trees of nearly equivalent length can be computed. Figure 20 depicts all of the trees derived from our character data that are of length 27 or less. There is one tree of length 24 (1a in Fig. 20) and this, like our favored tree depicted in Figure 19, also places the Cichlidae as the sister-group of the remaining Labroidei. Thus, the two shortest trees computed correspond in their placement of the Cichlidae, but differ as to which clade, the Embiotocidae or the Pomacentridae, forms the sister-group of the Labridae. No trees of length 25 can be derived from these data. Dia-

grams 2a-f and 3a-b (Fig. 20) represent trees of lengths 26 and 27 respectively. Of the trees represented in Figure 20, only 2a has been previously proposed as a labroid phylogeny (Kaufman and Liem, 1982; Stiassny, 1980). There are two trees of length 29, including the tree of Liem and Greenwood (1981), and two trees of length 30.

Given the plethora of possible trees of nearly equivalent length and yet widely varying topologies, it is clear that statements of relationship within the Labroidei must remain highly tentative. For this reason it would be ill-advised to propose any classificatory or nomenclatural changes based upon the results of our study. Perhaps the most significant observation we can make is that morphological character transformations within the Labroidei display a disconcertingly large amount of homoplasy. No matter which scheme of relationship is ultimately chosen, we must accept and acknowledge that in many structurally (and functionally?) disparate systems, character distributions within the Labroidei present a perplexing "web of parallelism." As systematic morphologists we are obviously interested in knowing whether the degree of homoplasy revealed in our study of the Labroidei is a general phenomenon that will be observed repeatedly in different groups that are subject to such detailed morphological analysis, or if the magnitude of the problem is peculiar to this group—and is therefore perhaps indicative of something particular about its morphological evolution.

We hope that future work incorporating other types of data, for example cladistically analysed physiological or biochemical data (Wiley, 1981), will provide a set of characters more clearly supporting a single phylogeny. Once such a single, highly corroborated phylogeny is available, then the same morphological homoplasy that proved an impediment to our understanding of the relationships of the group suddenly becomes of great poten-

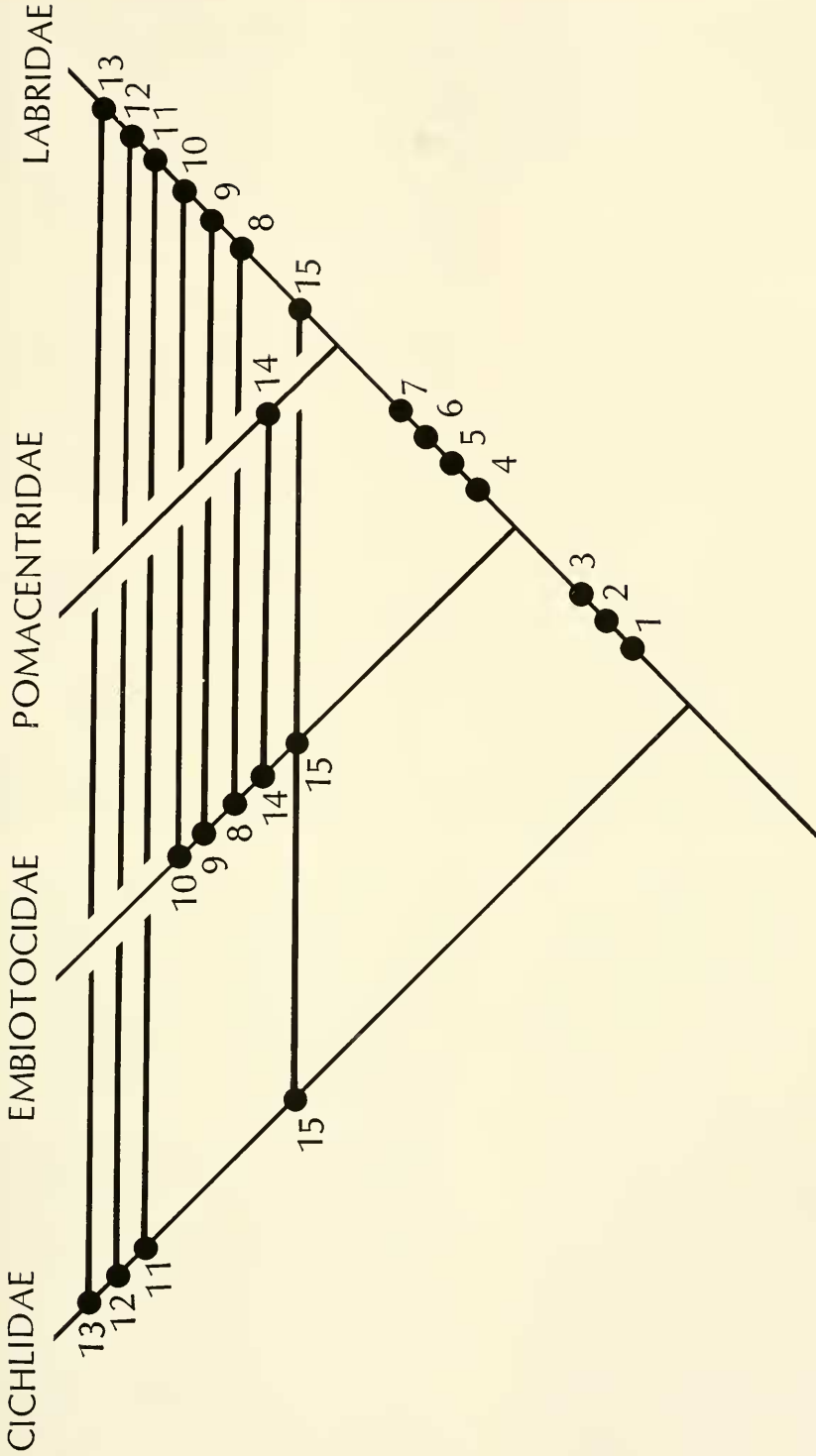


Figure 19. Cladogram of labroid relationships proposed in this study. Characters are: 1. LPJ with no trace of a central suture, and with pharyngeal teeth implanted directly over the midline. 2. Urohyal articulates with basibranchial one. 3. M. cranio-pharyngobranchialis 2 division of the transversus dorsalis muscle absent. 4. LPJ "Y-shaped" with short body and elongate lateral horns. 5. Obliquus ventralis IV and rectus ventralis V insert separately onto the semicircular ligament system. 6. Basibranchial one bears a large keel-like ventral extension. 7. Uroneural fused with the urostyle. 8. Second pharyngobranchial toothplate absent. 9. Fourth upper toothplate either markedly reduced or entirely lacking. 10. Interarcual cartilage absent. 11. Reduced number of caudal epurals. 12. Two of fewer predorsal bones. 13. Endopterygoid shelf absent and adductor arcus palatini inserts onto medial face of the suspensorium. 14. Extrascapular bone fused to the parietal. 15. Hemal arch of the antepenultimate caudal vertebra fused with the centrum.

tial use in extending our understanding of its evolution. Clades such as the Labroidei will provide an ideal opportunity for developmental geneticists, physiologists and morphologists to explore and elucidate the causal processes underlying morphological homoplasy.

DISCUSSION

Pharyngeal Complexity and Systematic Dominance

Of the eight characters found to diagnose the Labroidei, seven are elements of the PJA, and the eighth, although not obviously linked with the functioning of that apparatus, is a feature of the pharynx. Despite a conscious effort to locate additional synapomorphies in other structural systems we were able to find evidence of labroid monophyly only in the pharynx.

This predominance of PJA characters has not extended to our analysis of relationships within the Labroidei. Although features of the pharynx are well represented among the characters used, enough other characters from a reasonable "spread" of morphological systems are introduced so that pharyngeal information is not overwhelming at that level of analysis. Of the 15 characters used in the analysis of labroid intrarelationships (Figs. 19 and 20) only six are components of the PJA (characters 1, 3, 4, 8, 9 and 10). Three additional characters are located in the pharyngeal region but have no obvious functional connection with the PJA (characters 2, 5 and 6), and the remainder are distributed throughout the organism (characters 7, 11, 12, 13, 14 and 15). Despite the variety of sources of information regarding relationships within the Labroidei, we feel that the predominance of the pharynx as a source of information at the subordinal level is noteworthy and credits further consideration here.

When a particular morphological structure or functional complex plays such a disproportionately predominant role in the systematics of a group of organisms there

are several reasons why that region or complex may be of interest. While freely acknowledging that many non-morphological features can be of equal, and sometimes even primary, importance in the evolution of groups and their interrelationships (Mayr, 1969; Miller, 1949), we will restrict ourselves to a consideration of the particular morphological properties of groups:

1. The skewed emphasis may reflect an historical bias in the taxonomy of the group. For example, "caudal characters" may have traditionally (originally) been used in analyses and subsequent workers have followed the precedent and directed attention to the complex.
2. For some reason a particular region/character complex may be assessed a priori to be of no significance in the evolution of the group, and thus attention has been centered upon the region. This emphasis reflects what Mayr (1969) has termed the "Darwin Principle" in systematics and stresses the use of conservative, "non-functional/non-adaptive" characters in systematic analyses.
3. For some reason a particular region/character complex may be assessed a priori to be of particular significance in the evolution of the group, and thus attention has centered upon the region. This is the opposite position to the preceding case, and emphasizes the use of malleable "functional/adaptive" characters. Although few authors are explicit in their formulation of this approach it is implicit in the works of a number of functional morphologists (e.g., Dullemeijer, 1974; Gutmann, 1977) and "evolutionary" taxonomists (e.g., Szalay, 1981; see also discussion in Cracraft, 1981a).

Each of the above can loosely be viewed as resulting in some sort of taxonomically introduced bias, and subsequent investigation of other morphological complexes would render a range of additional characters for analysis and

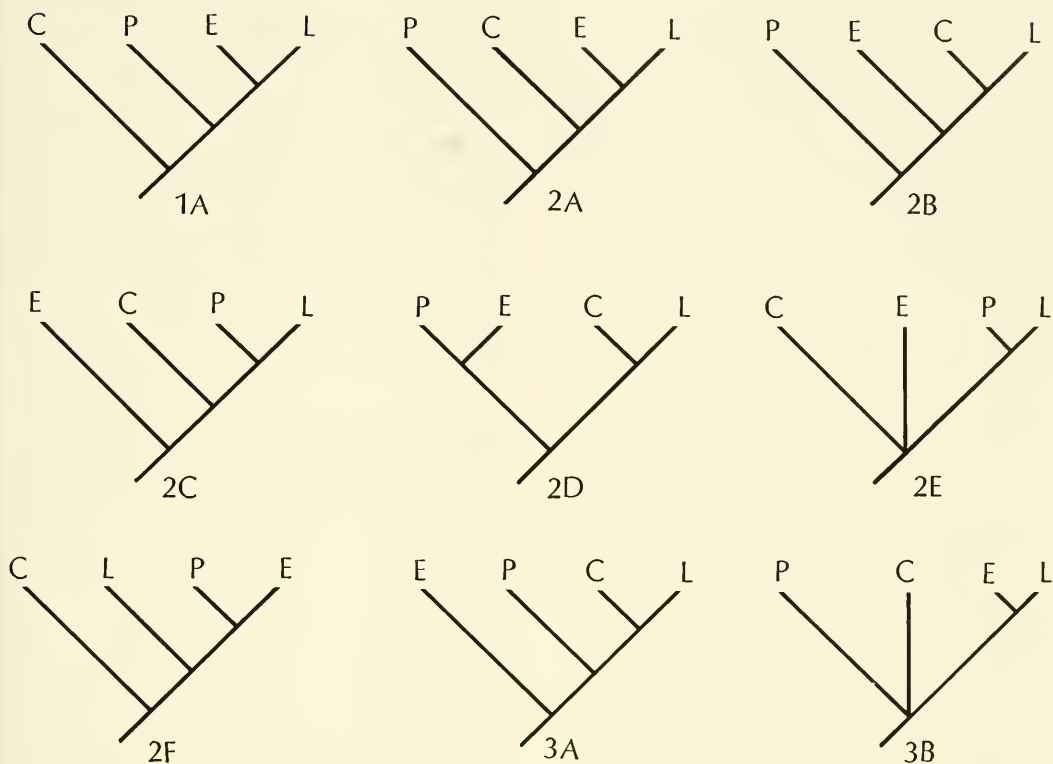


Figure 20. Range of additional trees (of length 27 or less) derivable from the character data entered into the analysis. 1A (length 24), 2A–F (length 26), and 3A–B (length 27). C = Cichlidae, P = Pomacentridae, E = Embiotocidae and L = Labridae.

the predominance of the original complex may be expected to be reduced. This isn't, of course, to say that those original features suddenly become unimportant or insignificant, but only that they no longer predominate.

In view of our conscious effort to locate features other than pharyngeal ones uniting the Labroidei and our inability to find any, we suggest that it is improbable that investigator bias is responsible for the importance of the pharynx in diagnosing the clade. Of course we cannot rule out the possibility that other morphological information does exist and that we have simply not found it yet, but our hypothesis is that such data do not exist.

4. Predominance of the region may simply be a reflection of structural (and/or functional) complexity. As Lauder

(1981) quite correctly pointed out, few morphologists have explicitly considered the influence of complexity upon patterns of morphological change. Intuitively at least, it seems that complex systems have a higher likelihood of change than simple ones. If complexity is defined as the number of parameters needed to describe form (Lauder, 1981; Vermeij, 1973), then an increase of complexity will automatically increase the number of possibilities for change in the component elements and in their relations to one another. Complex systems have more potentially stable intermediate states and have, therefore, options for change in design at each level (Lauder, 1981; Simon, 1962).

The euteleostean pharynx is a highly complex construction, composed of many elements and numerous struc-

tural and functional networks of interconnection. Lauder (1983) showed that there is a degree of decoupling between patterns of functional activity and the sequence of structural modification in the euteleostean pharynx. In this complex system overall functioning can be maintained in the face of sequential structural modification. In view of the complexity of the system, and concomitant structural variation, it is perhaps not surprising that so much attention has been centered upon pharyngeal characters in the systematics of euteleostean clades (e.g., Nelson, 1969; Rosen, 1973; Rosen and Parenti, 1981).

- We doubt whether a case can be made that the labroid pharynx is more complex than that of other clades; complexity alone does not seem to account for our observation of pharyngeal dominance in labroid systematics.
5. The predominance of any particular region/character complex may indicate that it actually represents some significant and independent locus of evolutionary change.

With all of the caution that the preceding list engenders, we would nonetheless like to speculate that our findings may indicate that the PJA does indeed represent precisely this sort of major locus of evolutionary change for the labroid clade. That features of the pharynx alone seem to characterize the Labroidei indicates that, relative to other systems, this complex underwent extensive restructuring early in the history of the clade. Perhaps, as suggested by Liem (1973), a single change in one aspect of this complex precipitated a major restructuring in other elements of the pharyngeal network. Initial restructuring of the pharynx, a complex considered to be profoundly important in the evolution of the Labroidei (see discussion of the concept of key innovation below), may then have been a very rapid, yet integrated, event.

If this is the case, the pharynx may eas-

ily be overemphasized as a source of *systematic* information since many of the characters treated as independent (and equivalent) are a necessary result of the single initial change. The remarkable mirroring of a whole suite of morphological features of the PJA in the phylogenetically disparate labroids and beloniforms would appear to support this inference. Recognition of what constitutes a "unit-character" in a situation such as this is obviously fraught with difficulty.

Key Innovations and the Explanation of Differential Diversity

According to recent studies, features of the pharynx may have had important consequences for the morphologic and taxic diversity of the Labroidei (e.g., Lauder, 1983; Liem, 1973, 1980; Liem and Osse, 1975; Liem and Sanderson, 1986). Early suggestions that the acquisition of a novel structure (e.g., an LPJ suspended by a muscle sling) could profoundly influence the subsequent evolution of a lineage usually involved the idea of the novel feature allowing entry into a new adaptive zone (e.g., Mayr, 1963; Simpson, 1944, 1953, 1959).

Subsequent radiation in an arena of reduced competition gave rise to diverse and/or speciose lineages, the success of which could then be attributed to the acquisition of the unique feature characterizing them. The importance of such an "adaptive breakthrough" in transspecific evolution and the origin of higher taxa has been repeatedly stressed in subsequent explanations of organismic diversity (and enhanced speciation?) (e.g., Jaanusson, 1981; Liem, 1973, 1980; Miller, 1949; Stanley, 1968). A plethora of names for this "distinctive sort of adaptation" (Simpson, 1953) is available (e.g., key adjustments, key inventions, key evolutionary novelties, major adaptive innovations). For ease of discussion we will follow Lauder (1981) in adopting the term key innovation (KI).

Most recently, in a pair of perceptive

and insightful publications Lauder (1981, 1982a) critically analyzed the key innovation concept. His primary criticism, with which we concur, is that a hypothesis that a structure plays a "key" (causal?) role in the subsequent evolution of a lineage is untestable within the framework usually proposed. If an evolutionary novelty is indeed unique, how can any hypothesis regarding its importance be tested by comparison with its influence in independent circumstances? Unique events do not allow a critical analysis of their consequences.

As a solution to this dilemma, Lauder (1981, 1982a) suggested that general attributes (emergent organizational properties) of unique features be sought, so that the consequences of these general features can be compared in both closely related and distantly related taxa. In this sense, it is not only the particular physical features located in compared taxa that are the putative KIs but also the general or emergent properties resulting from them. Lauder provided us with a method to bypass the evolutionary "uniqueness" of specific morphologies by concentrating attention on general, and thus comparable, properties. As an example of such a general property, Lauder (1981) discussed the decoupling of primitively constrained systems and its possible consequences on the subsequent evolution of a taxon. Precisely such a functional decoupling between buccal and pharyngeal jaws, following key innovational pharyngeal specialization, is proposed to have played a central role in the extensive trophic diversification of cichlid fishes (Liem, 1973; Liem and Osse, 1975). The development of a highly integrated PJA (later found to characterize the Labroidei as a whole, see pages 273–288), and the subsequent freeing of the buccal jaws from a major role in food preparation prior to deglutition (Liem's second major function), is held to have resulted in an extreme specialization of the buccal apparatus. ". . . The release of the restricting influence of the second major

function resulted in the emergence of numerous specializations of collecting mechanisms dealing with dramatically diverse foods." (Liem, 1973: 41). The resultant ability of the clade to exploit a great variety of trophic resources is considered to be of central importance in cichlid trophic diversification, ecological predominance, and explosive speciation (e.g., Fryer and Iles, 1972; Greenwood, 1974, 1984; Liem, 1973, 1980). If this particular PJA configuration was indeed an unique evolutionary novelty then no comparison of its effects in other clades would be possible and its consequences could not be assessed (but see discussion of the beloniform parallel on pages 310–312). However, as decoupling is a general or emergent property transcending the features of any particular system, one can legitimately look elsewhere for clades that exhibit comparable structural and/or functional decoupling. A relationship between decoupling and, for example, morphological diversity between terminal taxa of both clades can now be sought. Following Lauder (1981, 1982a; Liem and Wake, 1985), one may pose the relational hypothesis that the emergence of a general property (Z in Fig. 21A) has consequences for the diversity of terminal taxa (A–D in Fig. 21A). The proposed method of testing this hypothesis is the repeated assessment of diversity (or whatever parameter is being judged) within and between unrelated lineages also possessing this general property (Z' and Z", Fig. 21A). If no relationship between the presence of this property and a particular pattern is found, the hypothesis is rejected.

However, if such a comparative test is to be meaningful, one cannot directly compare attributes of the taxa in which the putative KIs occur. Diversity (like species richness) is a relative term and if a clade or set of clades is to be considered diverse (or speciose), this determination can only be made with respect to some meaningful standard of comparison. A consideration of the phylogenetic context of each taxon provides the only meaning-

ful standard for comparison. As is implicit in Hennig (1966: 225) and Lauder (1981, 1982a), it is the sistergroup of the taxon possessing the putative KI that provides the standard by which diversity (or species richness) may be judged (see also excellent discussion in Cracraft, 1981b, 1982).

We would like to emphasize the need for comparison between the clade possessing the putative KI and its sistergroup lacking it (A-D/X in Fig. 21B) in assessments of diversity or species richness. Accordingly comparisons of species number (or diversity) are made between clades that have equivalent histories up to the time of their divergence. They are of equal age, began with equivalent developmental programs, and differ only in those features arising (or re-emerging) after their divergence. In these important features then, the sistergroup is the closest approximation we have to what the lineage under consideration would be like had it not developed the KI (and other evolutionary novelties characterizing it). As illustrated by Figure 21B, testing of hypotheses regarding the role of a key innovation becomes a two step process. Step one (Fig. 21B) provides a measure of the relative diversity of the taxon possessing the putative KI (A-D in Fig. 21B) and its sister group (X in Fig. 21B). In the second step (step 2 in Fig. 21B) relative diversities are then compared *between* independent lineages in which comparable key innovations have arisen (Step 2 in Fig. 21B: E-H to X' versus I-L to X"). In this way possibly confounding historical factors are held to a minimum and the relative nature of the term diversity (or species richness) is acknowledged and, as far as is possible, is accounted for (but see discussion on pages 312-313).

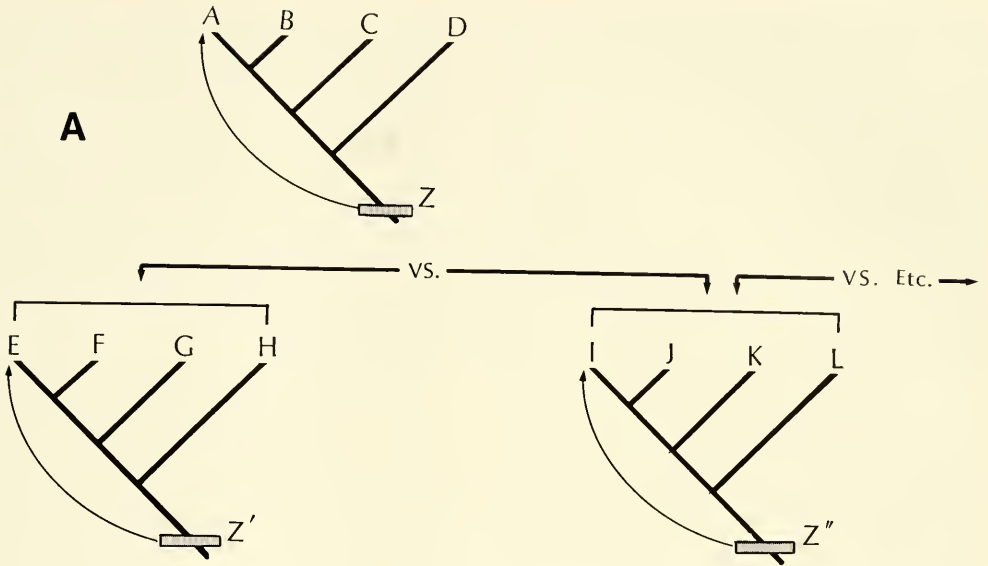
In past considerations of the key innovation concept it is frequently unclear what exactly the concept is meant to ex-

plain. A key innovation is frequently invoked to account for the success of a lineage, but many properties might be used to characterize a particular lineage as successful. For example, enhanced speciation rates, reduced extinction rates, or morphological diversification are all perfectly reasonable criteria of particular kinds of success. In discussions or hypotheses of a key innovation, species richness and morphological diversity are often used interchangeably or treated as if they are so closely related as to render distinction unnecessary. While it may frequently be the case that morphological differentiation is the by-product of the speciation process, it is by no means necessarily so, as is evidenced by the well-documented phenomenon of sibling species (Mayr, 1976; McKaye *et al.*, 1982). Nor is it necessarily the case that morphological diversity within a lineage can be explained simply as the sum of differentiations accompanying speciation (Simpson, 1944, 1953). Even if morphological diversity is the proposed outcome of the origin of a key innovation, it must also be clearly specified what types of features are in fact diversifying. Is it the specific morphological complex involving the key innovation or the organism as a whole that is supposed to undergo change? Any test of the effect of structural features or their emergent properties on the evolution of a lineage will require an explicit prediction of the nature of the consequences of their presence.

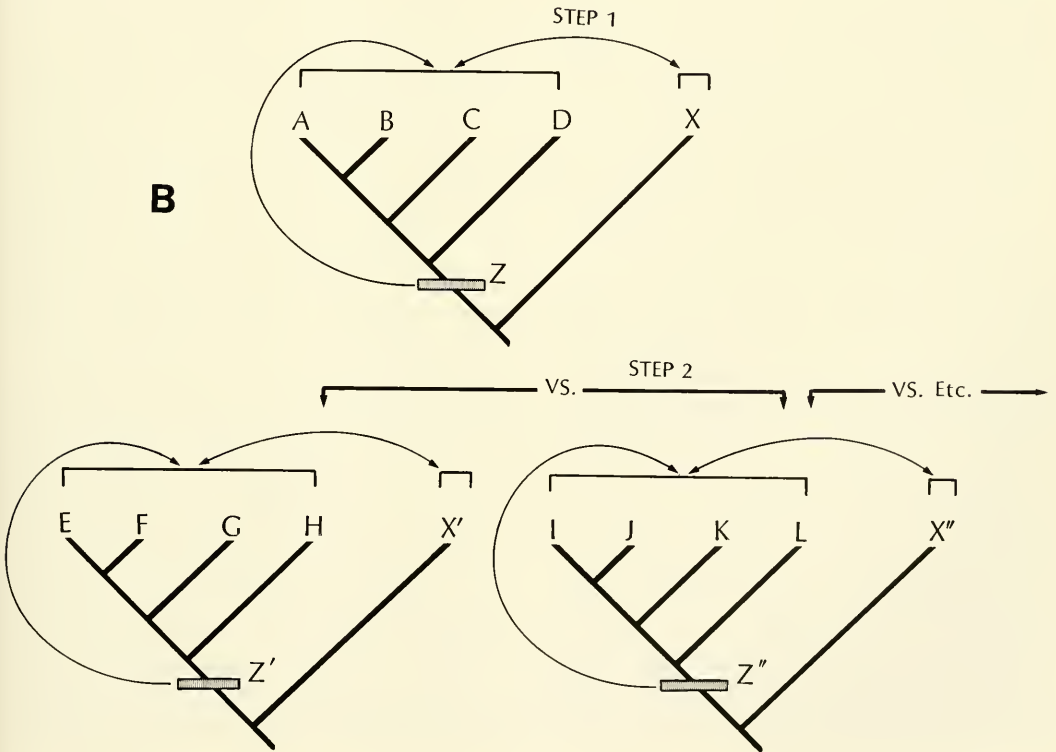
The need to precisely specify the nature of the predicted consequences of a key innovation is clearly evident when we consider the development of a pharyngeal muscle sling and Liem's (1973) hypothesis of its effect on subsequent evolution. As described on pages 274-266, within the Beloniformes, one finds a striking morphological parallel between the configu-

Figure 21. Testing of relational hypotheses involving correlations between the possession of emergent features (Z) and the resultant properties of groups. A. After Lauder (1981); B. Test incorporating initial intracladal sistergroup (X) comparison (step 1) prior to intercladal comparison (step 2). (see page 310 for further explanation of figure).

A



B



ration of the PJA of labroids (Fig. 6) and that of the Exocoetoidea (Fig. 2). In these fishes (the Hemiramphidae and Exocoetidae) the fourth levator externus muscle (and a portion of the levator posterior) form a muscle sling supporting the fused fifth ceratobranchial elements. In addition, the dorsal musculature (particularly the transversus dorsalis posterior) is reduced and the articulatory facets of the third pharyngobranchials are exposed to form a diarthrosis with a well-developed neurocranial apophysis (Fig. 2E). The Scomberesocidae lack these features although, like the Exocoetoidea, they possess a completely united LPJ in which no trace of a median suture is evident. The LPJ also bears a well-developed median keel onto which the transversus ventralis muscle inserts.

The fortuitous morphological mirroring of aspects of the labroid PJA by that of non-adrianichthyoid beloniforms allows at least one test of the evolutionary consequences of a putative key innovation in these phylogenetically disparate assemblages. However, for this test to be unambiguous we need a clearly stated hypothesis of the consequences of the key innovation. For example, if our prediction is increased species number, we find that the Exocoetoidea is indeed more successful than its sister lineage, the Scomberesocidae (Fig. 7; 135+ species in the Exocoetoidea versus 36 species in the Scomberesocidae, Nelson, 1984). This would seem to support the hypothesis of this particular pharyngeal configuration being key to the taxic success of a lineage. Likewise, if diversity of the trophic apparatus as a whole is the predicted outcome, then the wide range of tooth morphologies of both the PJA and the buccal jaws found in the Exocoetoidea relative to the Scomberesocidae (Collette, 1966, 1974, 1976; Parin, 1961) would lend support to this hypothesis. However, the Scomberesocidae exhibits a far greater diversity of LPJ form (but not dentition) than does its sister lineage (e.g., compare

figs. 2, 3 of Collette, 1966 with fig. 16 of Parin, 1961). In this respect, the Exocoetoidea can be considered to lack significant diversity, indicating that the development of a muscle sling has not resulted in an overall pharyngeal diversification. Thus it would seem that clarification and explicit statement of the proposed consequences of the development of the key innovation are a necessary prerequisite for the generation of hypotheses about generality of effects and the role of KIs in evolution.

Despite the methodological refinement of Lauder's scheme outlined here (Fig. 21B), rigorous testing of historical hypotheses still presents difficulties. Even given a reasonable number of independent clades in which to conduct comparisons, it seems unlikely that comparisons of lineages sharing a putative KI with their respective sistergroups (the first step in our analysis) will always lead to unambiguous statements regarding the role of those innovations in, for example, cladogenesis. If our hypothesis is that the presence of a key innovation is somehow implicated in enhanced speciation rates (or morphological diversification), this would be refuted by finding a clade with a comparable key innovation which is depauperate relative to its sistergroup. However, the question immediately arises as to how comparable these sister lineages are with respect to the suite of extrinsic factors acting upon them after their origin (see also Cracraft, 1982). Any differences in species richness or morphological diversity found in the two clades might as easily be the result of differences in their habitat (e.g., estuary versus coral reef), vicariant history (e.g., mid-ocean versus shallow lake basin), later behavioral developments, and so on. Almost inevitably there will be many ways in which the factors affecting species richness or diversity will differ due to the independent histories of sister lineages subsequent to their phylogenetic origin.

Likewise, the second phase of the analysis (i.e., comparison of independent clades

within which the key innovation arises; step 2 in Fig. 21B) presents its own difficulties. It might not be the case that the same evolutionary "novelty" or property will have equivalent effects when arising in different phylogenetic contexts. How likely is it that two different lineages, each with its own intrinsic morphological constraints, developmental pattern, etc. will respond in the same way to the appearance of the "same" evolutionary novelty or property? While each appearance of the evolutionary novelty would indeed be independent, it might not be comparable because the innovation would, in each case, appear against a unique historical background, a set of existing functional constraints, and would be subject in the course of subsequent evolution to a unique set of extrinsic factors. The consequences of, for example, decoupling in one component of the trophic apparatus (e.g., the buccal jaws) may be very different, depending on the limitations imposed by primitive constraints on other components of the trophic apparatus (e.g., pharyngeal jaws). While the first step of the analysis would not be affected, since the network of constraints would be primitive for both taxa (A–D and X; Fig. 21B), the nature of the constraints affecting independent taxa (E–H to X' vs. I–L to X"; Fig. 21B) might differ greatly and thus have different interactions with the putative key innovation. Even if an innovation may be implicated in cladogenesis (e.g., Stanley, 1975) or diversification in one case, in another case it might arise in a context in which pre-existing functional networks or subsequent environmental influences are so constraining as to overwhelm its role in diversification or cladogenesis. Thus, assertions about the influence of key innovations, even when situated in a strictly phylogenetic framework, run the risk of being reduced to particularistic explanations about unique events in an unique historical arena.

Despite the problems alluded to above, we concur with Lauder (1982b: 66) that

"The key to discovering the limits to deterministic explanation in the historical record will be the extent to which general historical pathways in the transformation of biological design are revealed by a phylogenetic analysis of structural and functional patterns." The structural approach to historical patterns advocated by Lauder renders phylogeneticists with a method with which to begin that search. Discovery of such general historical pathways will have profound implications regarding the nature of the evolutionary process.

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provoking, and it is with a profound sense of gratitude and loss that we dedicate this paper in his memory.

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APPENDIX 1

Data Matrix Used in Character Analysis

Taxa/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Plesiomorphic	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cichlidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
Embiotocidae	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1
Labridae	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Pomacentridae	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0

The characters are:

1. LPJ with no trace of a central suture, and with pharyngeal teeth implanted directly over the midline.
2. Urohyal articulates with basibranchial one.
3. Absence of musculus cranio-pharyngobranchialis 2 muscle.
4. LPJ "Y-shaped" with short body and elongate lateral horns.
5. Obliquus ventralis IV and rectus ventralis V insert separately onto the semicircular ligament system.
6. Basibranchial one bears a large keel-like ventral extension.
7. Uroneural fused with the urostyle.
8. Second pharyngobranchial toothplate absent.
9. Fourth upper toothplate either markedly reduced or entirely lacking.
10. Interarcual cartilage absent.
11. Reduced number of caudal epurals.
12. Two or fewer predorsal bones.
13. Endopterygoid shelf absent and adductor arcus palatini inserts onto medial face of the suspensorium.
14. Extrascapular bone fused to the parietal.
15. Hemal arch of the antepenultimate caudal vertebrae fused with the centrum.

APPENDIX 2

Abbreviations Used in Figures

AD5	Adductor 5	MT. P2	Transversus pharyngobranchialis 2
ART.Z	Articulation zone	NC. AP	Neurocranial apophysis
BB1-4	Basibranchial 1-4	PB1-3	Pharyngobranchial 1-3
BHY	Basihyal	PB3-TP	Pharyngobranchial 3 toothplate
CB1-5	Ceratobranchial 1-5	PB2-3-TP	Toothplate of PB 2-3
CL	Cleithrum	PB3-FC	Articulation facet of PB3
CT	Connective tissue	PHC.E	Pharyngocleithralis externus
"EHR"	"Epihemal ribs"	PHC.I	Pharyngocleithralis internus
EP1-4	Epibranchial 1-4	PHY	Pharyngohyoideus
EPR	Epipleurals	PR	Pleural rib
INTARC.C	Interarcual cartilage	REC.V	Rectus ventralis V
HBR	Hypobranchial	SEMICIRC.LIG	Semicircular ligament system
L.BB3/UHY	Basibranchial3/urohyal ligament	tA ₁	Tendon of A ₁ division of adductor mandibulae
LE4	Fourth levator externus muscle	TDP	Transversus dorsalis posterior
LE ₄ + OP	Fourth levator externus and obliquus posterior	TV IV-V	Transversus ventralis IV-V
LP	Levator posterior muscle	UHY	Urohyal
LPJ	Lower pharyngeal jaw	UP4	Fourth upper toothplate
LT. HORN	Lateral horn		
OBL IV	Obliquus ventralis IV		
OP	Obliquus posterior muscle		
MC. P2	Cranio-pharyngobranchialis 2		
MT. E2	Transverse epibranchialis 2		